Calorie restriction brings no benefits to lifespan under stochastic environments

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RSG conceived the idea; JAD, RSG and AA designed the methodology; JAD and PH collected and digitized data; JAD analysed data; JAD led the writing of the manuscript with assistance from RSG. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data in this paper are published open access in multiple formats (*e.g.*, .pdf, .R, .cpproj)

Abstract

The impacts of resource availability on senescence –the loss of vitality with age– are formalised under the Calorie Restriction (CR) theory, which predicts that the onset of senescence is delayed and life expectancy prolonged due to the ultimate effects of restricted resource intake without malnutrition. However, CR studies are largely implemented in unrealistic environments that do not consider how interacting, stochastic drivers impact longevity. Indeed, little is known about the impact of stochastic resource availability on senescence, even though environmental stochasticity is the norm rather than an exception in natural populations. Here, we examine whether and how stochasticity in the quantity, quality, and frequency of resources impact lifespan, life history trait trade-offs, and population structure in two long-lived planaria: *Schmidtea mediterranea* and *Dugesia tahitiensis*. For each species, we estimate weekly population size, survival, and a size distribution metric that quantifies population structure and skew. Over the 19-week study, survival in *S. mediterranea* is lower than *D. tahitiensis* across all feeding regimes. However, for both species, CR does not diminish survival. There are also no clear shifts in population structure over time across the different feeding regimes. For *S. mediterranea*, in most treatments, population structure changed to fewer smaller than larger individuals (right-skewed). In the case of *D. tahitiensis*, only treatments where resources are provided frequently cause right-skewed population structures. Population size also varied between species, with that of *D. tahitiensis* never declining across treatments, and always becoming larger than S. mediterranea; in the case of *S. mediterranea*, most treatments show a decline in population counts over the study period. As before, no clear pattern emerges in the changes in population counts under CR conditions for both species. As such, we did not find evidence of CR providing benefits in terms of lifespan nor trade-off between population counts, survival, and body size. We call for the careful re-evaluation of decades of CR work in short-lived species, by expanding and testing predictions in more realistic settings and across a wider range of life histories.

Keywords: ageing, diet, life history trait, longevity, planaria, population structure, senescence, trade-off, vitality

INTRODUCTION

Resource availability is a key driver of individual development and population performance (Stearns 1992; Ozgul *et al.* 2009; Smallegange 2011). Yet, studies on how resource availability impacts the life cycle of an organism have largely focused on specific life transitions (*e.g.,* age at maturity (Stearns 1992; Auer 2010; Smallegange 2011) or features of the life cycle (*e.g.,* reproduction (Williams 1996; Rutstein *et al.* 2005); survival (Ozgul *et al.* 2009)). An important trait that has lacked similar attention is senescence; the physiological decline of an organism's vitality with age that ultimately reduces reproduction and increases mortality risk. Reproduction and survival are key demographic processes of the life cycle of a species with variation in these processes defining life history traits (*e.g.*, age at maturity, net reproductive rate, longevity, etc.) which, in turn, result in life history strategies that impact individual fitness and the dynamics of a species (Roff 1992; Stearns 1992; Capdevila & Salguero-Gómez 2019). Life history theory predicts a trade-off in resource allocation between maintenance (development and survival), and reproductive output of individuals (Roff 1992; Stearns 1992). However, the impact of resource availability on demographic processes, and therefore on life history traits, is not straightforward (Mysterud *et al.* 2001; Maron *et al.* 2015). For example, winter climate has been shown to have an indirect effect on foraging conditions for red deer (*Cervus elaphus*) and domestic sheep (*Ovis aries*) in Norway (Mysterud *et al.* 2001). Mysterud *et al.* (2001) found that high North Atlantic Oscillation (NAO) values had a positive effect on individual body mass, a proxy for increased survival and reproduction in ungulates. Years of high NAO values correlates with increased warm and wet winters, and a potential mechanism explaining the response the authors found was that more snow in the high-elevation summer areas will provide prolonged periods of access to high-quality forage during summer.

Trade-offs in resource allocation between maintenance and reproduction form the predictions of two of the three main theories of senescence (Williams 1957; Kirkwood 1977). Currently the

87 impacts of resource availability on senescence are formalised under the Calorie Restriction (*CR*,
88 hereafter) theory. Under CR theory, life expectancy is extended and the onset of senescence delayed
89 due to restricted resource intake without malnutrition (Weindruch & Walford 1988). The benefits of
90 restricted resource intake are hypothesised to be mediated at the molecular and cellular level by
91 lowering molecular oxidative damage (Sohal & Weindruch 1996; Sanchez-Roman & Barja 2013) and
92 reducing free radical-induced cellular damage (Barja 2004; Fontana & Klein 2007). The predicted
93 effects of CR have been observed in several species, from yeast (Lin *et al.* 2002; Masoro 2005), to
94 invertebrates (Mair *et al.* 2003; Carey *et al.* 2005), and mammals (Weindruch and Walford 1988;
95 Masoro 2005; Colman et al. 2014). However, recently the benefits of CR have been brought to
96 question. Several studies have shown no effects on lifespan or senescence (Troen *et al.* 2007; Smith
97 *et al.* 2010), with others even showing negative impacts, *i.e*., shortening lifespan and accelerating
98 rates of senescence (Weithoff 2007; Fisher *et al.* 2017). Possible reasons for this diversity in results
99 include the lack of standardised protocols of nutritional demands (Cava & Fontana 2013; Deere et al,
100 in prep) and protein:carbohydrate ratio (P:C) of diets (*e.g.* in *Drosophila*, Lee et al. 2008). The
101 environment of an organism too plays a role in determining senescence. Recent work by Roper et al.
102 (2021) suggest that key life history traits (*e.g.*, adult body size) and ecology of the organism may be
103 vital in determining senescence outcomes.

104 The rich diversity of life history strategies is not well represented in CR research (Deere *et al.*
105 2020). This is particularly notable given the link between an organism's life history traits and its
106 ecology (Jansen *et al.* 2012; Arlettaz *et al.* 2017). Indeed, most studies exploring the impacts of CR on
107 senescence have focused on short-lived species, while CR studies on longer-lived species remain
108 scarce: one study on the grey mouse lemur (*Microcebus murinus*; Pifferi *et al.* 2018) and two studies
109 on the Rhesus monkey (*Macaca mulatta*); Colman *et al.* 2009; Mattison *et al.* 2012)). Other common
110 life history strategies are even less frequently examined in CR, such as the ability to reallocate

111 resources internally. For instance, in both the Galápagos marine iguanas (*Amblyrhyncus cristatus*)
112 (Wikelski & Thom 2000) and some Planaria (Child 1914; González-Estévez 2009) individuals can shrink
113 via the digestion of internal organs when resource are scarce and subsequently re-grow when
114 resources become more abundant. In both cases, this ability to shrink enhances survival.

115 Empirical investigations of CR impacts on senescence have been largely focused on constant
116 resource conditions. However, mimicking the environment to which an individual is typically exposed
117 is key to examine senescence outcomes (Koons *et al.* 2014; Roper *et al.* 2021). This consideration is
118 particularly important because environmental stochasticity is known to shape life history traits
119 (Stearns 1992; Pardo *et al.* 2013; Behrman *et al.* 2015), which in turn play a crucial role in population
120 structure and dynamics (Tuljapurkar & Orzack 1980; Tuljapurkar *et al.* 2003; Coulson *et al.* 2006;
121 Simmonds & Coulson 2015). As far as we are aware, there are only two studies that explicitly
122 investigate CR impacts on senescence in stochastic environments (*Drosophila*, Mair *et al.* 2003;
123 medfly, Carey *et al.* 2005). In them, longevity was extended under a stochastic feeding regime. In the
124 case of *Drosophila*, three reduced dietary treatments were initiated; one where flies received
125 reduced diet for the length of adulthood and two where fully fed flies were switched to reduced diet
126 during their adulthood. When fully fed flies were switched to reduced diets at day 14 or day 22 of the
127 experiment there was a reduction in age-specific mortality, equivalent to that in treatments where
128 diets were permanently reduced, when compared to treatments where flies were fully fed. The
129 medfly study was more complex in that 12 stochastic dietary treatment regimes were used.
130 Treatments varied in how sparse or dense the food available was and how persistent each food patch
131 was (e.g., available for one day or 10 days). In this study, nine of the 12 treatments showed an
132 increase in life expectancies compared to the full diet treatment. However, little can be gleaned from
133 two studies alone to determine how stochastic environments impact senescence in the face of CR.

134 Here, we contribute to fill in the gap of knowledge in CR research by examining the impact of

stochasticity of resources in two long-lived invertebrate species, the planarians *Schmidtea mediterranea* and *Dugesia tahitiensis*. We use these species to examine whether and how stochasticity in three different dimensions of resource availability (quantity, quality, and frequency) impact their lifespan, life history trait trade-offs, as well as population structure and dynamics. Specifically, we hypothesize that: (H1) In high quantity, low quality environments, population size will be larger, and individual size will be normally distributed**.** High quantity, low quality environments are richer in protein; these environments typically promote reproduction (Lee 2015) and in turn individuals attain shorter lifespans, which free up more resources for reproduction to improve population viability (Bayliss & Choquenot 2002); (H2) In low quantity, high quality environments, population size will be smaller, dominated by larger individuals skewing the population size structure to the right, thus leading to increased longevity but lower reproduction. Environments with fewer, but higher quality resources, will likely be dominated by larger individuals that outcompete smaller individuals (Szabo 2002; Ward *et al.* 2006). In it, available resources will be allocated to maintenance because, in organisms with indeterminate growth like planarians, energy allocation is typically prioritised for maintenance over reproduction and growth (Jokela & Mutikainen 1995); and (H3) Environments with a higher frequency and quality of resource availability will result in an increase in clonal reproduction and a larger population size. Where resource supply is high and constant, populations support higher numbers, which decrease population extinction risk (Bayliss & Choquenot 2002; Lande *et al.* 2003).

METHODS

Study system and stock culture

157 Planaria have unique life history traits. Most notably, the majority of planarians are able of
158 restorative and physiological regeneration due to injury or damaged/ sick cells (Elliott & Sánchez
159 Alvarado 2013). The replacement of damaged or sick cells also contributes to the typically long-lived
160 life history of planarians. Indeed, under favourable, constant conditions, planaria are potentially
161 immortal (Elliott & Sánchez Alvarado 2013). Planarians are also able to shrink when faced with
162 unfavourable conditions (Child 1914; González-Estévez 2009). Here, we use *Schmidtea mediterranea*
163 (Benazzi, Baguna, Ballister, Puccinelli & Del Papa, 1975) and *Dugesia tahitiensis* (Gourbault, 1977),
164 two closely related, freshwater planarian species from the order Tricladida that are easily reared in
165 the lab (Sousa & Adell 2018). The two species also differ in size with *D. tahitiensis* larger (≈10mm in
166 length) than *S. mediterranea* (≈5mm in length). *S. mediterranea* can reproduce sexually or asexually
167 whereas *D. tahitiensis* is an obligate asexual. We used asexual lines of *S. mediterranea* for our
168 experiments in order to directly compare the two species. Asexual reproduction in planaria occurs
169 via a process called binary fission that results in two genetically identical clones of smaller size from
170 the fissioning individual (Malinowski *et al.* 2017).

171 To form cultures, a clonal line of the wild type, asexual strain of *S. mediterranea* and *D. tahitiensis*
172 were initiated from long-term cultures maintained by the Aboobaker laboratory in the Department
173 of Zoology at the University of Oxford. The *S. mediterranea* cultures originate from the main
174 laboratory stock used worldwide, first collected from Monjuïc, Barcelona. *D. tahitiensis* originate
175 from the cultures in the Egger laboratory at the University of Innsbruck. A total of three stock cultures
176 per species were started with 10 individuals each. To explore the impact of three different
177 dimensions of resource availability, we increased initial numbers of planarians to ensure a large
178 sample size. Once a week, for three weeks, 10 individuals per species were taken from each culture
179 and two transverse amputations per individual were performed (thus forming three individuals)
180 following methods in Sousa and Adell (2018). In doing so all individuals were of a similar chronological
181 age and the potential age variance was reduced to three weeks which is significantly less than that

182 of individuals within the main laboratory stock. Once fissioned, during regeneration, polarity of their
183 body axes is maintained. This means that each fissioned piece conserves the anterior-posterior,
184 dorsal-ventral and medial-lateral axes and, as such, subsequent organogenesis (Elliott & Sánchez
185 Alvarado 2013). Individuals were reared in a mixture of distilled water and sea salt (Instant Ocean sea
186 salt, Aquarium Systems) at a concentration of 0.5g/L. Cultures were fed on organic calf's liver twice
187 a week; the liver was left for two hours in the containers before being removed to ensure full satiation
188 of individuals within the population. After removal, the water-salt mix was replaced and the
189 containers housing the cultures were cleaned to avoid potential infection through debris build-up.
190 This feeding regime frequency was sufficient to ensure continued fissioning of individuals and
191 increasing numbers in the cultures. Stock cultures were housed in six 30cm long × 30cm wide × 15cm
192 high plastic containers (3 for *S. mediterranea*, 3 for *D. tahitiensis*) within a climate room set at 20°C
193 and kept in 0:24hr light:dark regime. Populations were only exposed to low levels of light for short
194 periods of time during feeding and data collection.

195 **Experiment**

196 To test our hypotheses regarding how CR impacts longevity and its trade-offs with other life
197 history traits in stochastic environments, we randomly assigned populations to a full-factorial design
198 for each of the two species. This design included three resource factors: quality, quantity, and timing
199 (Fig. 1). Quality of resource had two levels, differing in energy content and relative protein-to-
200 carbohydrate ratio: high-quality (high carbohydrate level, *HQ* hereafter) *vs.* low-quality (low
201 carbohydrate level, *LQ* hereafter). The high-quality diet was based on organic calf's liver and the low-
202 quality diet on bloodworm. The protein-to-carbohydrate ratio indicates resource quality, with low
203 carbohydrate to protein content corresponding to poorer quality (Lee et al. 2008). The two diets
204 differed not only in their energy content (109 kcal/100g in the liver *vs.* 14 kcal/100g in the
205 bloodworm) but also in their relative protein-to-carbohydrate ratios (1:0.35 in liver *vs.* 1:0.17 in

206 bloodworm). Quantity of resources had three levels, which differed in the amount of calories
207 available in each feeding: standard calorie intake (*SI*: 0.001g/individual, representative of intake to
208 maintain laboratory populations (Jochen 2018)), restricted calorie intake (*RI*: 0.0005g/ind.), hyper-
209 calorie intake (*HI*: *ad libitum* which was at least 10 fold, approx. 0.01g/individual, that of the SI). We
210 always fed treatments the day after population counts and after photographs were taken (see below)
211 to ensure that counts were reflective of the previous feeding event. We based the amount of
212 resource provided a given week on the population counts of the previous day and the relevant
213 treatment (*i.e.*, total number of individuals multiplied by the resource weight for the specific
214 treatment). All resources were weighed to the nearest 0.0001g using an Adventurer Analytical
215 microbalance (Ohaus). After feeding, all the water-salt mix solutions were replaced in the populations
216 of all treatments. This step was essential to ensure an oxygenated solution and to prevent infection
217 from the solution mix that contained excess debris. In the *HI* treatment, resources were left for 2 h
218 before removal to ensure full satiation. Different combinations of resource quantity and quality were
219 provided in two different frequencies: even (*E*), once every 7 days, or delayed (*D*), every 14 days.
220 We replicated all treatments in the full factorial (n = 12 levels: 2 qualities: *HQ vs. LQ*; 3 quantities:
221 *RI*, *SI* & *HI*; 2 frequencies: *E vs. D*) five times for each species. A replicate consisted of a population
222 (25mm deep × 150mm Ø) containing 10 individuals each, henceforth referred to as a population (total
223 n = 600 ind/spp). For each population, individuals were randomly isolated from one of the three stock
224 cultures and placed in the population 7-8 days before the start of the experiment. During this time,
225 individuals were not fed to ensure that individuals across all treatments were in a similar starved
226 state at the start of the experiment. Treatment populations were randomised into three blocks
227 containing 20 populations per species per block. For each species, all experimental blocks lasted 19
228 weeks (133 days). Blocks were staggered in three different start dates due to the logistical constraint
229 of sampling all 60 populations on the same day, as such staggered blocks allowed a more logistically
230 feasible sampling of 20 populations per day. Block 1 of the experiment started on the 4th February

2020, and block 2 on the 30th April 2020. In the case of block 3, the start date for *S. mediterranea* and *D. tahitiensis* differed due to low numbers available for *S. mediterranea* from the original source. As such, block 3 for *D. tahitiensis* started on the 1st May 2020 and for *S. mediterranea* on the 19th June 2020. Part way through the experiment, due to the COVID-19 pandemic, the location of the experiment to be changed, while retaining the same environmental conditions. For further details of this change, see the Supporting Information.

Within each population, every week, survival and asexual reproduction (clonal reproduction) were estimated by counting all living and dead individuals. This was done to determine changes in population size, as we expect that, (H1) in high quantity/low quality environments population size will be larger, (H2) in low quantity/high quality environments population size will be smaller, and (H3) increased frequency of resources will result in increased clonal reproduction. Additionally, size (area in mm^2) of each individual flatworm within each population was measured to determine growth/shrinkage. Our expectations here are that, (H1) in high quantity/low quality environments individual size will be normally distributed, (H2) low quantity/high quality environments will be dominated by larger individuals, and (H3) increased frequency of resources will result in greater rate of size oscillation.

To estimate individual size, once a week, photos of each population were taken. We placed a population on an A4 size light table and within an opened bottomed box (to allow light through). The top of the box had an 8cm diameter aperture to allow for a camera lens. A Canon EOS 700D digital SLR camera and a Canon 18-135mm EFS lens were attached to a tripod (Vanguard Alta Pro 263AP) so the lens was facing downwards and protruding into the top aperture of the box. The lens was set at a constant height of 29cm above the population. The camera settings were constant and set manually at F5.6, ISO 200 and a shutter speed of 1/100.

Image digitization

255 To obtain size measurements of individuals, images taken during the experiment required
256 digitization and analysis. All images (n = 1,140) were digitized and analysed using the CellProfiler
257 software (Lamprecht *et al.* 2007). CellProfiler is flexible open-source software that allows processing
258 of batches of images automatically while allowing users to adjust settings to measure the phenotypes
259 of interest. Based on the user settings, the software identifies possible entities (here individuals of
260 planarian) within the image and calculates the relevant data (*e.g.*, area of an individual) (see SI and
261 Fig. S2). Image settings were selected depending on the species in question as there are significant
262 size differences between *S. mediterranea* and *D. tahitiensis*. Within the experiment, because *S.*
263 *mediterranea* individuals were of a much smaller size than *D. tahitiensis* that the required minimum
264 and maximum values of the parameters used to identify individuals in the image (the 'object diameter
265 identification' parameter) had to be set to values that differed from *D. tahitiensis*. The specific user
266 defined settings were then used for the relevant species. All settings were saved as CellProfiler
267 project files and are accessible to use via the online Supplementary Information (Smed.cpproj and
268 Dtah.cpproj). In the case of *D. tahitiensis*, the procedure differed slightly for week 19 for the high
269 quality even feeding treatments for all resource intakes (high, standard and reduced intake). Briefly,
270 due to the high number of individuals present where there were large discrepancies between the
271 number of individuals identified by the program and the count by hand, we randomly chose one
272 quarter of the population to analyse using the user defined settings within the CellProfiler project file
273 (Dtah.cpproj). For the populations showing large discrepancies, before an image was taken, if
274 individuals were clumped together, we allowed individuals time to move around freely and become
275 less aggregated. This ensured that when the photograph was taken individuals were more evenly
276 distributed within the population. Results were then extrapolated by reproducing the data obtained
277 from the analysed quadrant for the three quadrants not analysed, further details can be found in the
278 Supplementary Information. Finally, because the individual area data calculated by CellProfiler is

provided in pixel values, we converted all values into mm^2 by multiplying pixel values by a conversion factor (see Supplementary Information).

Survival analysis

To determine whether high quantity/low quality environments (H1) and increased frequency of higher quality resources (H3) results in decreased lifespan, and low quantity/high quality environments (H2) results in increased lifespan, we calculated weekly survival in each population for each species using a Bayesian framework. We modelled survival as a function of covariates using a Binomial multilevel model with a logit link function with adaptive priors (Eq. 1). Fixed covariates were population (*POP*; categorical with 60 levels corresponding to each of the populations in the experiment; 5 replicates per treatment), treatment (*T;* categorical with 12 levels) and block (*B;* categorical with three levels).

$$Survival_i \sim \text{Binomial}(n_{i-1}, p_i)$$

$$logit(p_i) = \alpha_{POP[i]} + \beta_{T[i]} + \gamma_{B[i]}$$

$$\alpha_{POP} \sim \text{Normal}(\alpha, \sigma_{POP})$$

$$\beta_T \sim \text{Normal}(\alpha, \sigma_T)$$

$$\gamma_B \sim \text{Normal}(\alpha, \sigma_B)$$

$$\alpha \sim \text{Normal}(0, x)$$

$$\sigma_{POP} \sim \text{Exponential}(1)$$

$$\sigma_T \sim \text{Exponential}(1)$$

$$\sigma_B \sim \text{Exponential}(1) \qquad (1)$$

To fit the model in Eq. (1), we used the package "rethinking" (McElreath 2020) in the software R version 4.0.3 (R Core Team 2020). We then applied the model to each week of the experiment separately to determine weekly survival (as opposed to survival at the end of the experiment after 19 weeks), with the exception of week 1, as this week was the start of the experiment and so there was 100% survival in all populations. In this way, we could identify if at a specific point (*i.e.*, week) a significant reduction in survival occurred or if a constant decline in survival occurred over the 19 weeks. The model calculates the mean log-odds of survival between two given consecutive weeks where $Survival_i$ represents the number of individuals surviving in week *i* out of an initial count the week prior, n_{i-1}. Models for each week only differed in the standard deviation (x) of the α prior. The expectation was that, across weeks, populations (replicates of all treatments) would show variation in the standard deviation in the prior for each population's intercept (α). As such, not all weeks had the same x value, for each week *i* the value of x of the α prior was varied and a model comparison was done to ensure best model fit (models with the lowest WAIC values and highest weight value were taken as best fit). Final α priors for each model are provided in the supplementary information (final models used are in bold, Deere et al_SI_Model_comparisons.pdf). To calculate expected survival probability, predicted log-odds values were transformed using the logistic transformation.

To provide insight into how weekly changes in size distribution may impact survival probability at any given week, we calculated a *change in survival index (f)*, which assesses how survival in a given week compares to that of the previous week across treatments. To do so, we subtracted survival probability in week *i* +1 from survival probability in week *i*. Any value above zero would indicate an increase in survival probability from one week to the next, any value below zero would indicate a reduction in survival probability from one week to the next. As we expect population size to be higher

in high quantity/low quality environments (H1) and low quantity/high quality environments (H3), values in these environments should be below zero.

Size distribution analysis

To test whether individual body size is normally distributed (H1) in high quantity/low quality environments, (H2) dominated by larger individuals in low quantity/high quality environments, we used the size spectrum of populations as a method of quantifying the distribution of body size (Edwards *et al.* 2017). To do so, we calculated the size spectra slope values (*b*) for each population, of both species, across treatments following Carvalho et al. (2021). Briefly, here *b* describes the relative abundance of a population in relation to body sizes, thus providing a good proxy to quantify the distribution of body size within a population. A steeper (more negative) *b* indicates fewer large-bodied and/or more small-bodied individuals, which is an indication of a right-skewed size population structure. Values of *b* can vary substantially with estimates ranging from -6.75 to -0.40 been reported (Arranz *et al.* 2021; Carvalho *et al.* 2021). To estimate *b*, for each species separately, we used the abundance density function (Carvalho *et al.* 2021):

$$N(x) = nx^b \left(\frac{b+1}{x_{max}^{b+1} - x_{min}^{b+1}} \right) \quad (2)$$

where n is the number of individuals, x is the area of each individual (mm^2), x_{max} and x_{min} are the maximum and minimum area of individuals that were digitized. To calculate the maximum and minimum values, all populations for each treatment were pooled and maximum and minimum values were calculated separately for each treatment for each week.

For each week of the experiment, *b* values were calculated using the area measurements of each individual within each population. We then took the mean *b* for the five populations of each treatment to represent the weekly *b* value. As such, *b* indicates how the populations responds to the

varying quality, quantity, and frequency of resources provided and here is also used to examine potential trade-offs between weekly changes in size and survival. As with the survival analysis, we applied a Bayesian framework to determine changes in the mean *b* values using the R package "rethinking". To model *b* as a function of covariates, a Gaussian model with an identity link function was used (Eq. 3), with treatment (*T*, categorical with 12 levels) and week (*W*, 19 weeks) as fixed variables.

$$Size_i \sim \text{Normal}(\mu_i, \sigma)$$

$$\mu_i = \alpha_{T[i]} + \beta_{W[i]}$$

$$\alpha_T \sim \text{Normal}(\alpha, \sigma_T)$$

$$\beta_W \sim \text{Normal}(\alpha, \sigma_W)$$

$$\alpha \sim \text{Normal}(0, 0.5)$$

$$\sigma_T \sim \text{Exponential}(1)$$

$$\sigma_W \sim \text{Exponential}(1)$$

$$\sigma \sim \text{Exponential}(1) \qquad (3)$$

The model in Eq. (3) predicts the posterior mean size spectra slope value (*b*). We applied the model to the estimated mean *b* values, as described above, and within the model we varied standard deviation in the α prior as the expectation is shrinkage and regrowth of individuals across treatments. The standard deviation values of the α prior that were used for comparison were 0.05 and 1. We then conducted a model comparison to ensure best model fit; models with the lowest WAIC values and highest weight values were taken as best fit (see SI Table S1).

Population size analysis

To determine whether (H1) high quantity/low quality environments and (H2) low quantity/high quality environments result in a smaller population size, and whether (H3) increased frequency of higher quality resources result in a larger population size, we calculated changes in weekly population counts for each species. We applied a Bayesian framework to determine changes in population counts using the same "rethinking" R package as before. Population counts were modelled as a function of covariates using a Poisson multilevel model with a log link function using adaptive priors (Eq. 4), with treatment (*T*, categorical with 12 levels), week (*W*, 19 weeks) and block (*B*, 3 blocks) as fixed variables.

$$Counts_i \sim Poisson(\mu_i)$$

$$\mu_i = \alpha_{T[i]} + \beta_{T[i]} * w_{T[i]} + \gamma_{B[i]}$$

$$\alpha_T \sim \text{Normal}(2,1)$$

$$\beta_T \sim \text{Normal}(0, 0.2)$$

$$\gamma_B \sim \text{Normal}(2, 0.5) \qquad (4)$$

The model in Eq. (4) predicts the posterior mean population count. We applied the model to the population counts for all blocks and varied the mean and standard deviation in the α_T prior. Following the model simulations based on the various mean and standard deviation values, we conducted a model comparison to ensure best model fit (models with the lowest WAIC values were taken as best fit, see SI Table S2). The model with the best fit had a mean value of 2 and standard deviation value of 1 for the α_T prior.

391

392 **RESULTS**

393 **Survival analysis**

394 We predicted that (H1) in high quantity/low quality environments, and (H3) in environments with
395 increased frequency of resources lifespan would decrease, while (H2) in low quantity/high quality
396 environments lifespan would increase. Survival of *S. mediterranea* was most impacted by week of
397 the experiment rather than CR treatment; in it, for all treatments, weekly mean proportion survival
398 was generally high (0.65 – 0.92) but it did decline over the course of 19 weeks across all treatments
399 (Fig. 2). There was little difference in survival between treatments across all weeks, with weekly mean
400 log-odds of survival similar for all treatments (Fig. S3 - S5). Where few exceptions did occur, and
401 differences between treatments were found, these were largely in the high-quality resource (HQ)
402 treatments (Fig. S3 - S5). In the case of *D. thaitiensis*, survival was also mostly impacted by week
403 rather than CR treatment. The weekly mean proportion survival was generally high (0.54 – 0.91),
404 although there was less of an overall decline in mean proportion survival over the 19 weeks of the
405 experiment compared to *S. mediterranea*. However, proportion survival did fluctuate more between
406 weeks than *S. mediterranea* (Fig. 3). As with *S. mediterranea*, there was little difference in survival
407 between treatments across all weeks and treatments had similar weekly mean log-odds of survival
408 (Fig. S6 – S8). The one exception was week 13, where the log-odds of survival for the high-quality
409 treatments with delayed feeding having lower log-odds of survival than those of the high-quality
410 treatments that had even feeding (Fig. S7). However, for several of the weeks, the variation in log-
411 odds of survival across experimental blocks was greater than across treatments (Fig. S6- S8). A closer
412 examination shows that, for both species, block 1 had a larger impact on planarian survival than
413 treatment for several weeks, although the weeks where this impact was seen differed between
414 species (*S. mediterranea,* Fig. S3 - S5; *D. thaitiensis*, Fig. S6 – S8).

415 For both species no treatment showed a consistent pattern in survival index (*f*) (Fig. 4). This index
416 assessed how survival in a given week compared to that of the previous week across treatments.
417 However, *D. tahitiensis* had higher variation in the change in survival index than *S. mediterranea*. In
418 general, even feeding regimes showed less variation in *f*, and values were closer to zero, across
419 weeks, than delayed feeding regimes. Similarly, in HQ treatments, *f* was less variable, and values were
420 closer to zero, compared to low quality resource (LQ) treatments.

421

422 **Body size distributions**

423 We predicted that body size will be (H1) normally distributed in high quantity/low quality
424 environments, (H2) dominated by larger individuals in low quantity/high quality environments, and
425 (H3) that increased frequency of resources will result in a greater rate of size oscillation. Over time,
426 size spectra slope values (*b*) for *S. mediterranea* became more negative for most treatments (Fig. 2),
427 implying a more right-skewed population. From week 1 to week 13, there was a consistent decline in
428 *b* values, indicating a change in the size structure of the populations with an increase in smaller
429 individuals and fewer larger individuals. From week 14, however, size structure remained similar until
430 week 19. Overall, there was greater variation in size structure over time (Std. deviation: Week (*b*) =
431 0.24, 89% compatibility intervals (5.5% - 94.5%) (CPI) = 0.10 – 0.24) than between treatments (Std.
432 deviation: Treatment (*b*) = 0.16, CPI = 0.17 – 0.32) (Fig. S9). In the high quality treatments only the
433 even feeding standard intake and even feeding reduced intake treatments did not show a change in
434 size structure (i.e., no decline in *b* values) through time, while all other high quality treatments had
435 more right skewed populations at the end of the experiment compared to the start. This outcome
436 suggests that in high quality treatments, populations changed in size structure with an increase in
437 the number of small individuals and a decrease in the number of larger individuals over time (Fig. 2).
438 However, in the case of the low quality treatments, only the even feeding high intake and even

439 feeding standard intake treatments did not show a change in size structure at the end of the
440 experiment compared to the start. The remaining low quality treatments showed a change in size
441 structure with more right skewed populations at the end of the experiment compared to the start
442 (Fig. 2).

443 For *D. tahitiensis*, size spectra slope values (*b*) reflected populations that were less right skewed
444 in size structure throughout the experiment, with the even feeding treatments having more negative
445 values (*i.e.*, more right skewed) than all other treatments (Fig. 3). Compared to *S. mediterranea*, *D.*
446 *tahitiensis* populations were less right skewed but did fluctuate more between weeks. Overall,
447 variation in size structure over time (Std. deviation: Week (*b*) = 0.16, CPI = 0.11 – 0.22) and between
448 treatments (Std. deviation: Treatment (*b*) = 0.16, CPI = 0.10 – 0.24) were similar (Fig. S10). In the high
449 quality resource treatments only the even feeding treatments showed a change in size structure with
450 more right skewed populations at the end of the experiment compared to the start. In contrast, the
451 delayed feeding treatments showed little to no change in size structure of the populations (Fig. 3).
452 For the low quality treatments, changes to the size structure of populations to more right skewed
453 populations by the end of the experiment only occurred in the even feeding high intake and even
454 feeding standard intake treatments (Fig. 3).

455

456 **Population trends**

457 We predicted that in (H1) high quantity/low quality environments (H1.1) and low quantity/high
458 quality environments population will decline, and that in (H3) an increased frequency of resources
459 clonal reproduction will increase, resulting in increasing populations. Overall, *D. tahitiensis*
460 populations had higher numbers than populations of *S. mediterranea* at the end of the experiment
461 (Fig. 5). Population counts of *S. mediterranea* varied between treatments that differed in resource

462 quantity (*HI*: high intake*, SI*: standard intake*, RI*: reduced intake) and frequency (*D*: delayed, *E*: even)
463 but not resource quality (*HQ*: high quality*, LQ*: low quality) (Fig. 5A & B). The exception being the high
464 intake resource quantity treatments with even feeding (HI-E). In this case, the *HQ-HI-E* treatment,
465 where the resource was of a high quality, the population initially increased but then declined
466 compared to the *LQ-HI-E* treatment, where the population increased linearly over time (Fig. 5A & B,
467 Table 1). All populations where resource was delayed showed a decrease in population counts over
468 time compared to even feeding populations, where counts either stayed constant (*HQ-RI-E*, *LQ-RI-E*)
469 or increased over time (*HQ-SI-E, LQ-HI-E, LQ-SI-E*) (Fig. 5A & B, Table 1). Again, the exception being
470 the *HQ-HI-E* treatment where population counts declined over time.

471 In *D. tahitiensis*, populations either increased or remained stable (Fig.5C & D). When comparing
472 *HQ* and *LQ* treatments, *HQ* treatments with even feeding, regardless of resource quantity, had higher
473 population counts than *LQ* treatments with even feeding. When resource was delayed there was no
474 clear trend; the *HQ-HI-D* treatment had lower counts than the *LQ-HI-D* treatment, *HQ-SI-D* had higher
475 counts than *LQ-SI-D* and *HQ-RI-D* had similar counts to *LQ-RI-D* (Fig.5C & D, Table 2). For both species,
476 experimental block 1 had population growth rates lower than block 2 and block 3 (*S. mediterranea*:
477 block 1 - estimate -0.2, std dev. 0.13; block 2 - estimate 0.49, std dev. 0.13; block 3 - estimate 0.45,
478 std dev. 0.13. *D. tahitiensis*: block 1 - estimate 0.98, std dev. 0.2; block 2 - estimate 1.66, std dev. 0.2;
479 block 3 - estimate 1.55, std dev. 0.2). However, for all treatments, the population response
480 (increasing, decreasing or stable counts) of block 1 did not differ from that of block 2 or block 3 (Fig.
481 5, Table 1 & 2).

482

483 **DISCUSSION**

484 A comprehensive understanding of the impact of calorie restriction (CR) on senescence and
485 longevity has been hampered by the lack of realism in empirical manipulations (Deere *et al.* 2020)
486 and narrow focus on short-lived species (but see Colman *et al.* 2009; Mattison *et al.* 2012; Pifferi *et*
487 *al.* 2018). Here, we begin to address this shortcoming by incorporating stochasticity in resource
488 availability in a long-lived species. Our findings suggest that the fundamental predictions of CR do not
489 hold when multiple factors interact with reduced calorie intake. CR theory predicts extended
490 organismal longevity due to reduced calorie intake (Weindruch & Walford 1988). However, our
491 results show that for both of our study species survival is not affected by any moment of resource
492 availability: frequency, amount, or quality. Our findings suggests that interaction effects of these
493 three moments plays a significant part in the extent to which CR can be beneficial.

494 The exact way these moments in resource availability impacts survival is context dependent. A
495 possible reason for the variable responses we report could be the choice of quality of diet, with our
496 treatments lacking a more graduated component, in terms of variation in macronutrients, to the
497 quality of the resource provided. Indeed, in studies where the ratio of macronutrients have been
498 varied, in addition to calorie manipulation, the macronutrient ratios have a greater impact on
499 longevity than when manipulating calories (Lee *et al.* 2008; Solon-Biet *et al.* 2014). The response we
500 report here is also likely driven by the specific life history of planarians. Planarians have the unique
501 ability to restore damaged cells (Elliott & Sánchez Alvarado 2013). However, restoring damaged cells
502 is costly and requires resources and, if most resources are used for maintenance, less resources will
503 be available for reproduction.

504 The reduced reproduction and high survival within populations are indicative of the fundamental
505 trade-off between survival and reproduction under variable environmental conditions (Stearns
506 1992). In general, for *S. mediterranea* a trade-off between survival and reproduction can be seen
507 across the delayed feeding regimes but not for even feeding regimes. For *D. tahitiensis*, only

508 populations of low quantity and delayed feeding show a trade-off between survival and reproduction.
509 This begs the question, for populations of both species, where there is a lack of trade-off between
510 survival and reproduction do we see a trade-off with body size, another key life history trait?

511 When considering body size, our findings showed that the size structure of populations varied
512 across treatments. For *S. mediterranea*, populations become more right skewed across all treatments
513 (with two exceptions when feeding is even). The right skewed populations signify an increase in the
514 number of smaller individuals and fewer larger individuals in the populations (Carvalho *et al.* 2021).
515 Such changes in the population structure can occur when there is increased reproduction, as more
516 recruits of a smaller size enter the population. *S. mediterranea* reproduce asexually through fission
517 where larger individuals fission into two, with the anterior product (new recruits) generally smaller
518 than the posterior fission product (now a smaller asexual individual) (Peter *et al.* 2001). Thus, the
519 fissioning process results in fewer larger individuals and an increase the number of smaller
520 individuals. However, the right skewed size structure in populations as a consequence as a result of
521 reproductive events, will only be reflected in populations that are increasing in number. Where *S.*
522 *mediterranea* populations show a decline, the change in structure is not driven by reproduction and
523 in turn the new recruits in the population. Here, the life history of planaria is driving the response. A
524 key trait in the life history of planaria is the ability to shrink when food resources become scarce
525 (Mangel *et al.* 2016), with individuals experiencing up to a 50-fold change in size (Rink 2013).

526 The ability to shrink allows individuals to survive resource scarce environments until conditions
527 improve and resources increase. In planaria, when shrinkage occurs, cell numbers reduce through
528 autophagy, during which energy resources are supplied to neoblasts (stem/regenerative cells)
529 (Romero & Baguñà 1991; González-Estévez 2009). This process ensures maintenance levels of
530 individuals can be met. In our study, *S. mediterranea* populations which are more right skewed in size
531 structure have relatively high survival at the end of the experiment. The proportion survival of these

532 right skewed populations is above 0.6 and the change in survival index is consistently close to zero,
533 indicating survival from one week to the next is consistent. Shrinkage is a strategy found in several
534 taxa and mitigates the impact of fluctuating or stochastic environments on individual survival (Ebert
535 1967; Levitan 1988; Marinovic & Mangel 1999; Salguero-Gómez & Casper 2010, 2011). Indeed,
536 shrinkage has been shown to maintain survival during periods of resource scarcity. In the Galápagos
537 marine iguanas (*Amblyrhynchus cristatus*), individuals shrink up to 20% of their body length when
538 food resources are low during El Niño events (Wikelski & Thom 2000); those individuals that shrink
539 more have a higher rate of survival, pointing to the adaptive value of shrinkage. When food resources
540 improve during La Niña events, body length increases, as is the case with planarians when they
541 receive increased food resources after periods of low food (Child 1914; González-Estévez 2009;
542 Thommen *et al.* 2019).

543 The shrinkage seen in *S. mediterranea* populations is unlikely occurring in populations of *D.*
544 *tahitiensis*. Indeed, fewer *D. tahitiensis* treatments showed populations becoming more right skewed
545 over the course of the experiment. Where populations become more right skewed, the populations
546 do not show a decline in population size and, as is the case with *S. mediterranea*, changes in
547 population structure are likely due to fissioning. The populations of *D. tahitiensis* that have a less
548 right skewed size structure all increased in size over the course of the experiment and individuals are
549 likely experiencing increased competition for resource. The increased competition among individuals
550 for available resources results in contest competition, where an individual interferes with other
551 individuals to obtain resources (Nicholson 1954).

552 In competitive environments where contest competition occurs, smaller individuals can be
553 outcompeted by other larger individuals within the population as larger individuals are dominant
554 (Petersson & Järvi 2000; Stewart & Tabak 2011). In a study by Petersson & Järvi (2000) on brown
555 trout (*Salmo trutta*), the authors found that sea-ranch trout had higher dominance than wild-type

556 trout and that individuals with higher dominance had larger body sizes. In our study, contest
557 competition results in differences in average resource intake among individuals, with larger
558 individuals able to consume more resources per feeding event. As such, competition between two
559 individuals will result in the larger of the two increasing in size thereby increasing the number of
560 larger individuals in the population, resulting in less right-skewed populations.

561 The differences found in survival between *D. tahitiensis* and *S. mediterranea* can be attributed
562 to differences in a unique life history strategy of planaria; the ability to regenerate. Regeneration is
563 a life history strategy that can mitigate the impact of stochastic environments on longevity more than
564 restricting calories. The generally higher survival in *D. tahitiensis*, compared to *S. mediterranea*, is
565 likely due to *D. tahitiensis* being able to repair damaged cells more efficiently. *Dugesia tahitiensis* is
566 considered to have one of the highest regenerative and fissioninig capacities, and the most
567 stem/regenerative cells (neoblasts) within the Tricladida taxon (Baguñá & Romero 1981; Peter *et al.*
568 2001). High neoblast density in the parenchyma (the cellular tissue between the body wall and
569 organs) is a prerequisite for efficient regeneration after fission and, when compared to *S.*
570 *mediterranea*, *D. tahitiensis* have high cell counts (Peter *et al.* 2001). Moreover, neoblast self-renewal
571 activity can be impacted by food availability with reduced food levels resulting in lowered self-
572 renewal activity (Mangel *et al.* 2016). Reduced neoblast self-renewal activity will then enhance the
573 negative impacts experienced by *S. mediterranea*.

574 An additional, unintentional, contributing factor of the response of *S. mediterranea* to stochastic
575 environments may be due to the popularity of *S. mediterranea* as a model organism. *Schmidtea*
576 *mediterranea* is a well-known laboratory system (Sousa & Adell 2018) and the populations used in
577 our study have been maintained in the lab for >10 years (Aboobaker, pers. comm.). In contrast, the
578 populations of *D. tahitiensis* used in our study have not been maintained in the laboratory for such
579 an extensive period (< 10 years) (Aboobaker, pers. comm.). Given that our *S. mediterranea*

580 populations have been lab bred for such an extensive period, and in stable conditions, they may be
581 more vulnerable to unstable conditions than *D. tahitiensis*. The impact of generational lab breeding
582 is not uncommon and can have an impact on the response of individuals to experimental treatments
583 (Hoffmann & Ross 2018). A review, of the rates and patterns of laboratory adaptation of insects and
584 other invertebrates, found that laboratory-adapted lines tend to be more sensitive to stress,
585 indicating that stress-related traits experience relaxed selection (Hoffmann & Ross 2018). In the case
586 of *S. mediterranea*, the regeneration capabilities under stressful resource conditions have likely
587 become less effective due to the extensive period of lab breeding, a response not seen in *D.*
588 *tahitiensis*.

589 Life-histories differences between short- and long-lived species will ultimately have
590 consequences for CR predictions. There are few CR studies on long-lived species (*i.e.*, species that live
591 > 5 years), with studies showing benefits to longevity of CR (*e.g.,* Colman *et al.* 2009; Pifferi *et al.*
592 2018) and others not (*e.g.*, Mattison *et al.* 2012). Here we show that two long-lived species do not
593 conform to the predictions of CR. Indeed, we go further by highlighting that, in our study, both long-
594 lived species under stochastic environments do not conform to CR predictions. Our findings are
595 especially important in the face of CR research, largely as much of the fundamental work have been
596 on short-lived species in constant environments (*e.g.*, McCay *et al.* 1935; Sanchez-Roman & Barja
597 2013). An exciting opportunity now arises. Moving forward CR research needs to extend the
598 important CR work done in short-lived species, that identified mechanisms and pathways impacting
599 aging, to include long-lived species in stochastic environments. Such a move is key, as the
600 mechanisms and pathways previously identified may not be the same as those present in species that
601 are long-lived.

602

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Table 1. Model estimates of log population counts for *Schmidtea mediterranea*. Mean estimate, standard deviation and compatibility interval (5.5% and 94.5%) values are given for treatments and all blocks. Model diagnostic criteria are given by n_eff (estimate of number of independent samples) and Rhat4 (Gelman-Rubin convergence diagnostic of the Markov chains, values of Rhat4 that are above 1.00 indicate chains have not converged). HQ indicates high quality diet; LQ indicates low quality diet; HI indicates high food intake; SI indicates standard food intake; RI indicates reduced food intake; D indicates delayed feeding (every 14 days) and E indicates even feeding (every seven days).

Treatment	Mean	SD	5.50%	94.50%	n_eff	Rhat4
Intercept: HQ_RI_D	2.47	0.14	2.24	2.70	2710.50	1.00
Intercept: HQ_RI_E	2.51	0.14	2.29	2.74	2599.08	1.00
Intercept: HQ_SI_D	2.50	0.14	2.27	2.72	2608.47	1.00
Intercept: HQ_SI_E	2.40	0.14	2.18	2.62	2619.35	1.00
Intercept: HQ_HI_D	2.75	0.14	2.52	2.97	2652.59	1.00
Intercept: HQ_HI_E	2.73	0.14	2.51	2.96	2628.85	1.00
Intercept: LQ_RI_D	2.76	0.14	2.53	2.98	2684.96	1.00
Intercept: LQ_RI_E	2.36	0.14	2.13	2.58	2663.23	1.00
Intercept: LQ_SI_D	2.76	0.14	2.54	2.98	2572.94	1.00
Intercept: LQ_SI_E	2.50	0.14	2.28	2.72	2566.11	1.00
Intercept: LQ_HI_D	2.61	0.14	2.38	2.84	2755.66	1.00
Intercept: LQ_HI_E	2.37	0.14	2.15	2.59	2617.55	1.00
Slope: HQ_RI_D	-0.03	0.01	-0.04	-0.02	40550.55	1.00
Slope: HQ_RI_E	0.01	0.00	0.00	0.02	45941.15	1.00
Slope: HQ_SI_D	-0.01	0.00	-0.02	0.00	44231.03	1.00
Slope: HQ_SI_E	0.02	0.00	0.01	0.03	48917.31	1.00
Slope: HQ_HI_D	-0.05	0.01	-0.05	-0.04	40107.92	1.00
Slope: HQ_HI_E	-0.04	0.00	-0.05	-0.03	45798.84	1.00
Slope: LQ_RI_D	-0.05	0.01	-0.06	-0.04	42787.15	1.00
Slope: LQ_RI_E	0.00	0.01	-0.01	0.01	43362.26	1.00
Slope: LQ_SI_D	-0.03	0.00	-0.04	-0.02	47043.00	1.00
Slope: LQ_SI_E	0.03	0.00	0.02	0.04	51516.00	1.00
Slope: LQ_HI_D	-0.08	0.01	-0.09	-0.07	37311.66	1.00
Slope: LQ_HI_E	0.02	0.00	0.01	0.02	44358.27	1.00
Block: 1	-0.20	0.13	-0.41	0.01	2357.12	1.00
Block: 2	0.49	0.13	0.28	0.70	2330.43	1.00
Block: 3	0.45	0.13	0.24	0.66	2337.87	1.00

Table 2. Model estimates of log population counts for *Dugesia tahitiensis*. Mean estimate, standard deviation and compatibility interval (5.5% and 94.5%) values are given for treatments and all blocks. Model diagnostic criteria are given by n_eff (estimate of number of independent samples) and Rhat4 (Gelman-Rubin convergence diagnostic of the Markov chains, values of Rhat4 that are above 1.00 indicate chains have not converged). HQ indicates high quality diet; LQ indicates low quality diet; HI indicates high food intake; SI indicates standard food intake; RI indicates reduced food intake; D indicates delayed feeding (every 14 days) and E indicates even feeding (every seven days).

Treatment	Mean	SD	5.50%	94.50%	n_eff	Rhat4
Intercept: HQ_RI_D	1.37	0.21	1.04	1.70	697.41	1.00
Intercept: HQ_RI_E	1.13	0.21	0.80	1.46	684.28	1.00
Intercept: HQ_SI_D	1.38	0.21	1.05	1.71	678.31	1.00
Intercept: HQ_SI_E	1.48	0.20	1.15	1.81	667.32	1.00
Intercept: HQ_HI_D	1.58	0.20	1.25	1.90	680.42	1.00
Intercept: HQ_HI_E	1.41	0.20	1.08	1.73	670.42	1.00
Intercept: LQ_RI_D	1.38	0.21	1.05	1.72	701.68	1.00
Intercept: LQ_RI_E	1.33	0.21	1.00	1.66	691.70	1.00
Intercept: LQ_SI_D	1.37	0.21	1.04	1.69	693.81	1.00
Intercept: LQ_SI_E	1.25	0.21	0.91	1.58	684.99	1.00
Intercept: LQ_HI_D	1.53	0.20	1.21	1.86	677.28	1.00
Intercept: LQ_HI_E	1.55	0.20	1.22	1.87	667.50	1.00
Slope: HQ_RI_D	0.00	0.00	-0.01	0.01	11537.49	1.00
Slope: HQ_RI_E	0.08	0.00	0.07	0.08	11261.76	1.00
Slope: HQ_SI_D	0.04	0.00	0.04	0.05	10501.34	1.00
Slope: HQ_SI_E	0.10	0.00	0.09	0.10	14156.41	1.00
Slope: HQ_HI_D	0.03	0.00	0.02	0.03	11558.86	1.00
Slope: HQ_HI_E	0.09	0.00	0.09	0.10	14856.58	1.00
Slope: LQ_RI_D	-0.01	0.00	-0.02	0.00	9902.21	1.00
Slope: LQ_RI_E	0.02	0.00	0.01	0.02	9904.69	1.00
Slope: LQ_SI_D	0.01	0.00	0.01	0.02	10919.98	1.00
Slope: LQ_SI_E	0.06	0.00	0.05	0.07	11058.69	1.00
Slope: LQ_HI_D	0.06	0.00	0.05	0.06	15235.21	1.00
Slope: LQ_HI_E	0.09	0.00	0.09	0.10	13912.86	1.00
Block: 1	0.98	0.20	0.66	1.30	651.85	1.00
Block: 2	1.66	0.20	1.33	1.98	653.85	1.00
Block: 3	1.55	0.20	1.23	1.88	652.12	1.00

Figure legends

Figure 1. Full factorial experimental design. Design has three resource factors: quality, quantity and timing. Resource quality has two levels (top right panel): high quality (*HQ*; orange dots) and low quality (*LQ*; purple dots). Resource quantity has three levels (middle right panel): restricted intake (*RI*; single grey dot), standard intake (*SI*; three grey dots) and hyper caloric intake (*HI*; six grey dots). Resource timing has two levels (bottom right panel): even feeding (*E*; every seven days – black line), delayed feeding (*D*; every 14 days – grey line). Each population was initiated with 10 individuals and replicated five times resulting in a total of 600 individuals and 60 populations per species. Populations were counted and photographed weekly.

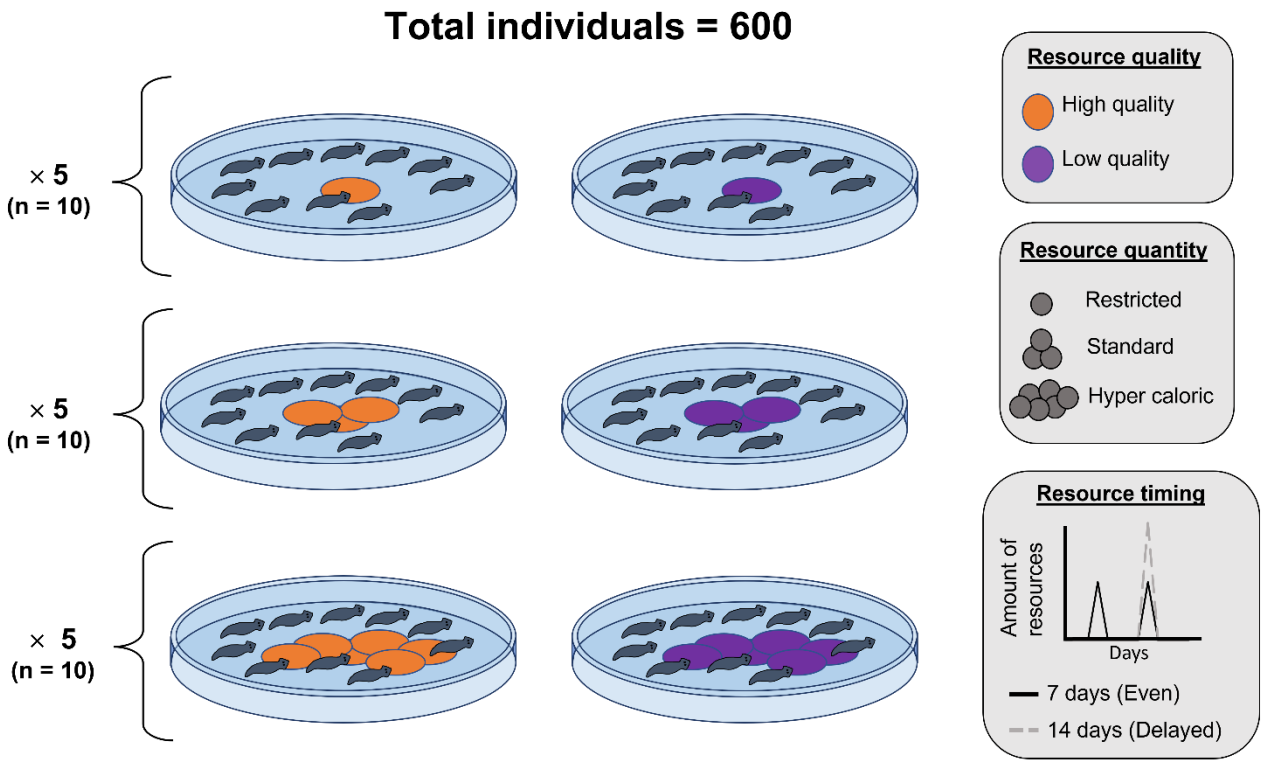
Figure 2. Survival in *Schmidtea mediterranea* populations is high and consistent across treatments however population structure changes across time in most treatments. Weekly proportion survival and size spectra slope values (*b*) for *S. mediterranea*. A) Median estimated size spectra slope (*b*) values (black points) with 95% confidence intervals (black bars), and median estimated proportion survival (red lines) with 89% compatibility intervals (dashed red line) for high quality (*HQ*,) treatments over 19 weeks. B) Estimated size spectra slope (*b*) values (black points) with 95% confidence intervals (black bars), and median estimated proportion survival (red lines) with 89% compatibility intervals (dashed red line) for low quality (*LQ*,) treatments over 19 weeks. Left panels indicate delayed feeding treatments and right panels even feeding treatments. Top panel represent high intake (*HI*,), middles panel standard intake (*SI*,) and bottom panel reduced intake (*RI*,) treatments.

Figure 3. Survival in *Dugesia tahitiensis* populations is high and consistent across treatments with little change in structure to populations. Weekly proportion survival and size spectra slope values (*b*) for *D. tahitiensis*. A) Median estimated size spectra slope (*b*) values (black points) with 95% confidence intervals (black bars), and median estimated proportion survival (red lines) with 89% compatibility intervals (dashed red line) for high quality (*HQ*,) treatments over 19 weeks. B) Estimated size spectra slope (*b*) values (black points) with 95% confidence intervals (black bars), and median estimated proportion survival (red lines) with 89% compatibility intervals (dashed red line) for low quality (*LQ*,) treatments over 19 weeks. Left panels indicate delayed feeding treatments and right panels even feeding treatments. Top panel represent high intake (*HI*,), middles panel standard intake (*SI*,) and bottom panel reduced intake (*RI*,) treatments.

Figure 4. Week to week survival is largely consistent across treatments but varies between species. Change in survival index values of *S. mediterranea* over the 19 weeks for A) high quality (*HQ*,) treatments and B) low quality (*LQ*,) treatments. Change in survival index values of *D. tahitiensis* over the 19 weeks for C) high quality (*HQ*,) treatments and D) low quality (*LQ*,) treatments. Values (proportion survival at *t+1* minus proportion survival at *t*) are shown for high intake (*HI*,) treatments (top panel), standard intake (*SI*,) treatments (middle panel), and reduced intake (*RI*,) treatments (bottom panel). Red points indicate estimated proportion survival from the model and black points indicate data points. Dashed line indicates the zero line, values above the line indicate an increase in survival probability from one week to the next, any values below the line indicate a reduction in survival probability from one week to the next.

Figure 5. Population size differs between species but with no clear patterns across treatments. Weekly population size of *S. mediterranea* over the 19 weeks for A) high quality ( ) treatments and B) low quality ( ) treatments. Weekly population size of *D. tahitiensis* over the 19 weeks for C) high quality treatments and D) low quality treatments. Solid black line indicates mean population counts for all five replicates (across all blocks) of the raw data for a given week. Dashed line indicates the mean estimated population counts for block 1, dotted line the mean estimated population counts for block 2 and the two-dash line the mean estimated population counts for block 3. Shaded grey regions indicate 89% compatibility intervals (5.5% - 94.5%). Left panels indicate delayed feeding treatments and right panels even feeding treatments. Top panel represent high intake (*HI*,), middles panel standard intake (*SI*,) and bottom panel reduced intake (*RI*,) treatments.

842 **Figure 1**



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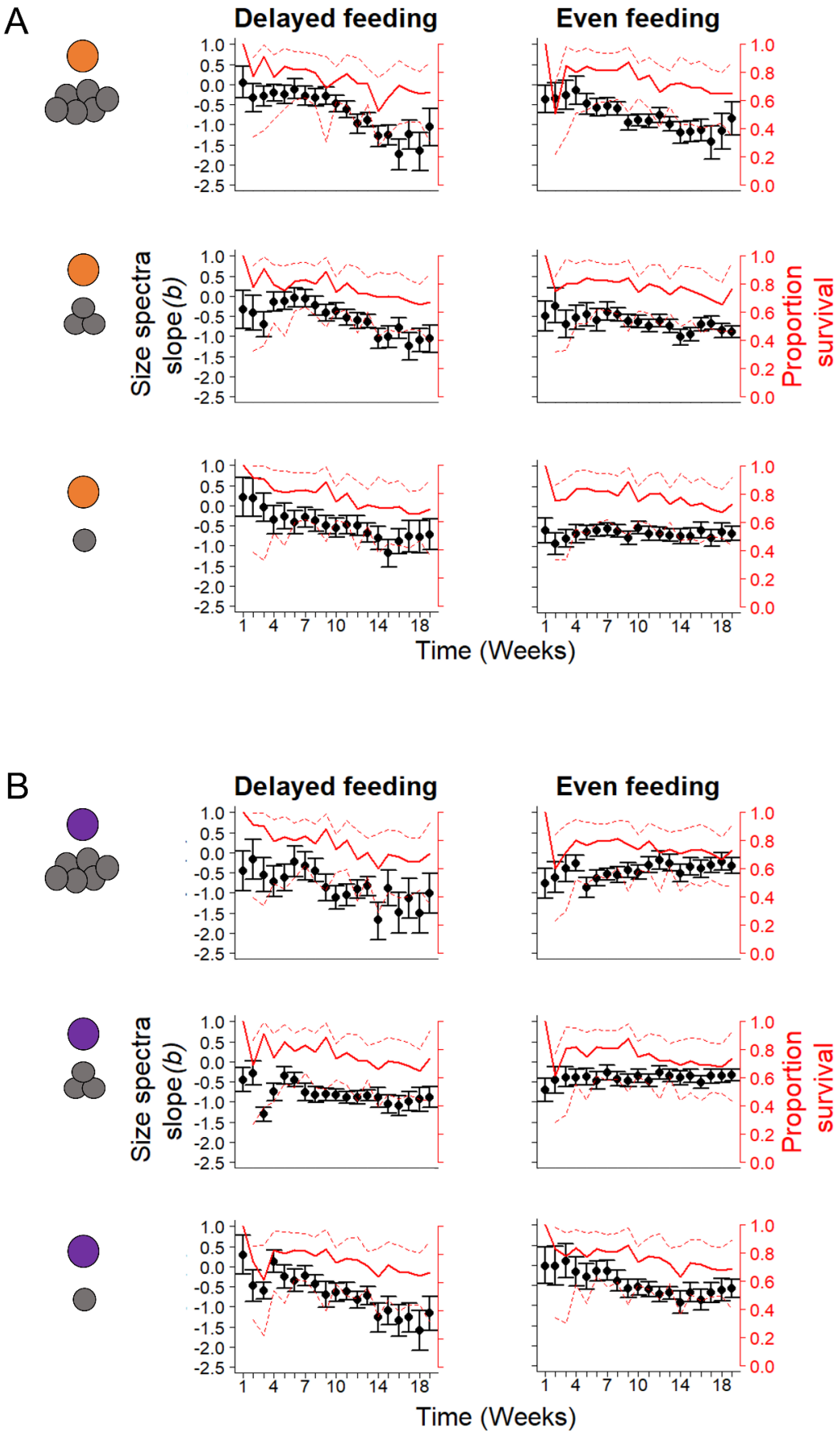
851 **Figure 2**



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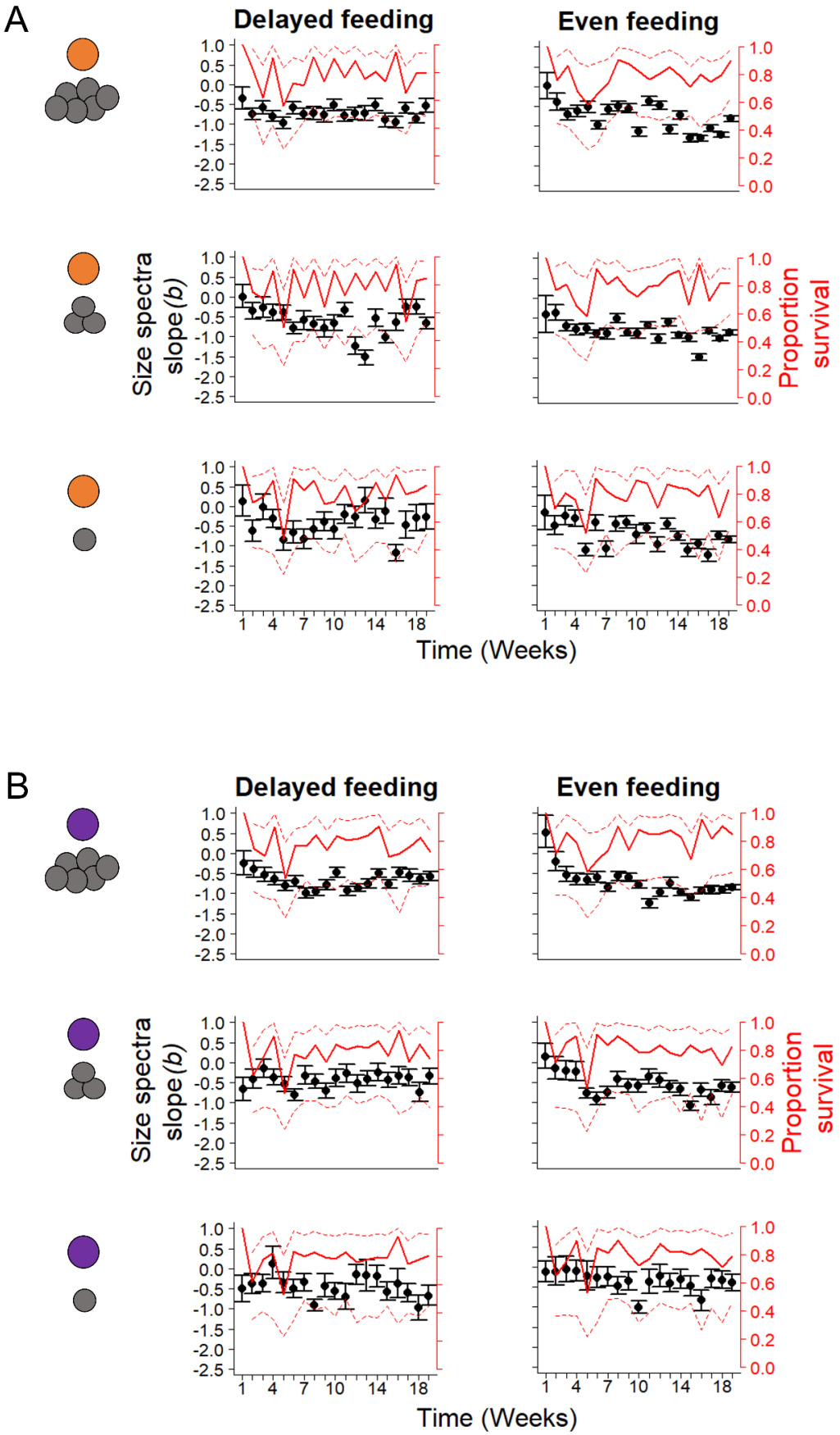
853 **Figure 3**



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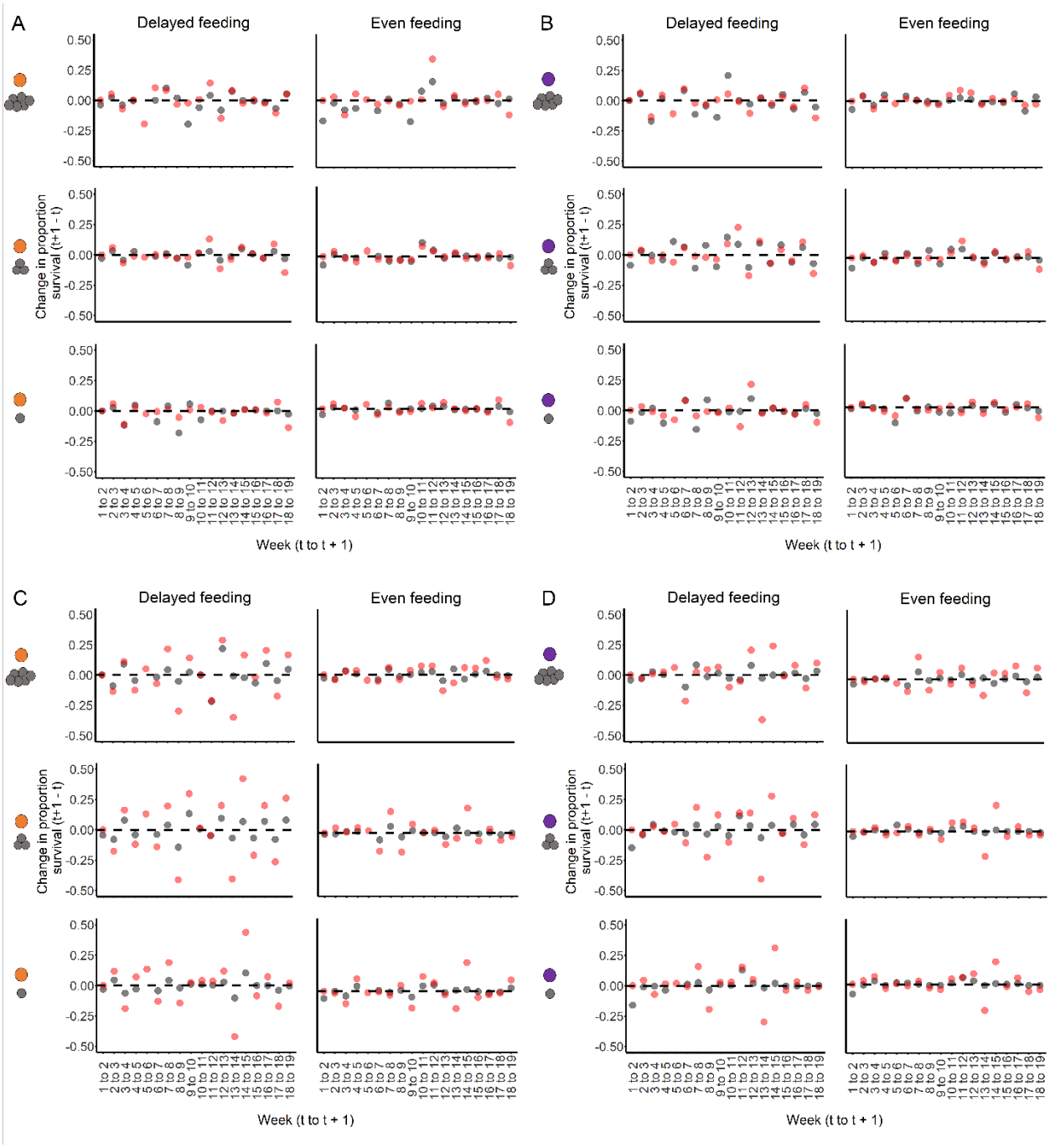
855 **Figure 4**



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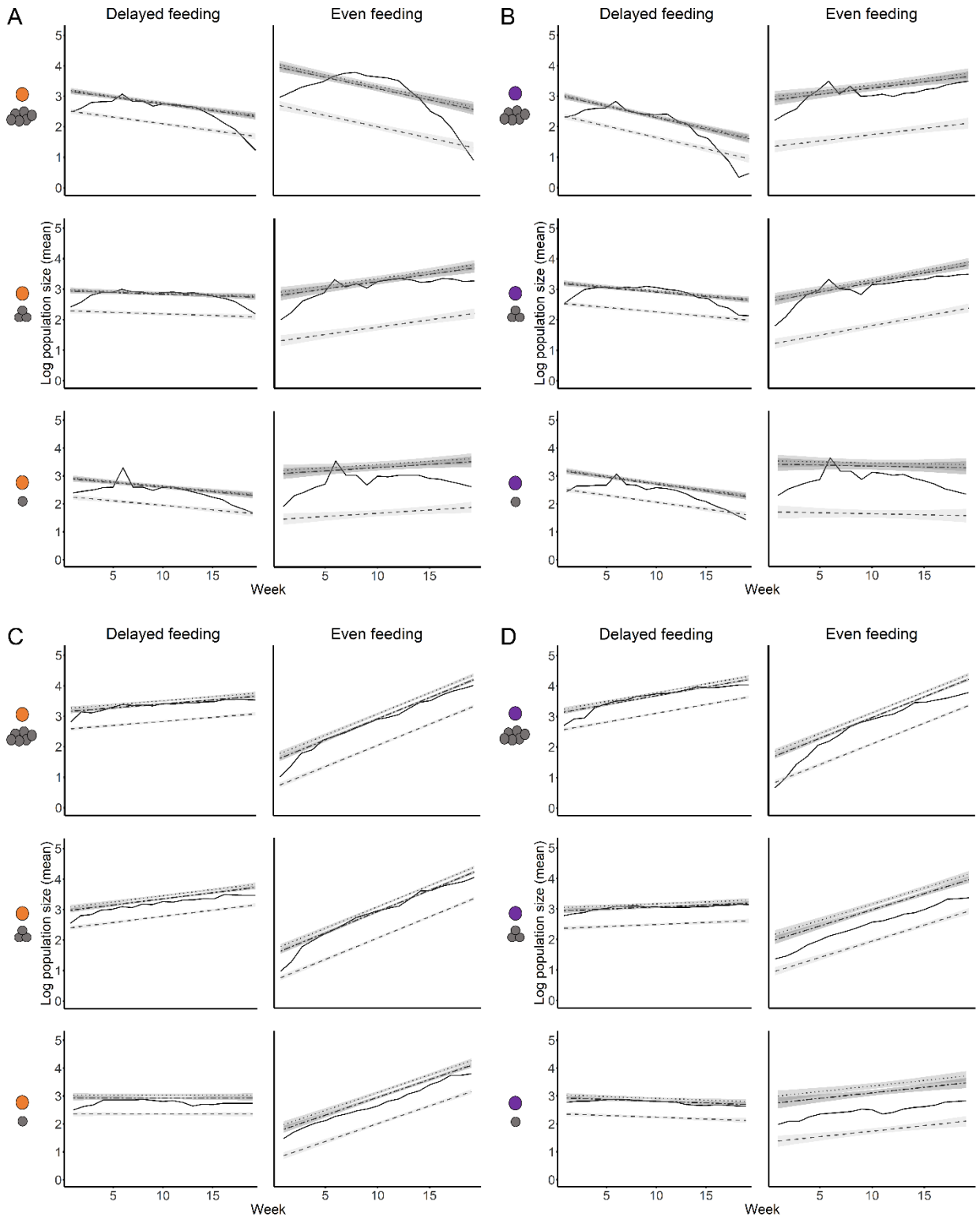
858 **Figure 5**



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