

1 **A future food boom rescues the negative effects of cumulative early-life adversity**  
2 **on lifespan in a small mammal**

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22 **SIGNIFICANCE**

23 Harsh early-life conditions influence health and survival during adulthood, but the  
24 factors that can ameliorate these effects remain ambiguous. Here, we show that the  
25 consequences of early-life adversity on longevity in squirrels are rescued by a high-  
26 quality environment later in life if such benefits are had by the entire population.

27 Providing individuals with supplemental food increased lifespan, but did not modify the  
28 relationship between early-life adversity and lifespan. However, squirrels that  
29 experienced a population-wide future food boom lived longer than squirrels that did not  
30 despite early-life adversity. Our findings suggest that individual resilience to early-life

31 adversity may hinge on population-level patterns of competition and energetic  
32 constraint, and thus on the quality of the future environment beyond the individual.

33

## 34 **ABSTRACT**

35

36 Challenging or adverse early-life conditions, even when transient, can have long-lasting  
37 effects on individual phenotypes and reduce lifespan across species. If these effects  
38 can be mitigated, even in part, by a high quality later-life environment, then differences  
39 in future resource access may explain variation in vulnerability and resilience to early-  
40 life adversity. Using 32 years of data on 886 wild North American red squirrels, we test  
41 the hypothesis that the negative effects of early-life adversity on lifespan can be  
42 mitigated by later-life food abundance. We first define early-life adversities as factors  
43 that significantly reduce the likelihood of juvenile survival, and find that they had  
44 cumulative negative effects on lifespan. We then show that although experimental  
45 supplementation with additional food increases individual lifespan, it did not change the  
46 consequences of early-life adversity on longevity. A naturally-occurring future food  
47 boom experienced in the second year of life, however, did eliminate the longevity costs  
48 of a harsh early-life environment. Together, our results demonstrate that adverse  
49 conditions experienced early in life reduce lifespan in red squirrels and thus may  
50 influence patterns of natural selection beyond juvenile viability. That these effects can  
51 be mitigated by a high-quality future environment suggests a non-deterministic role for  
52 early-life conditions on later-life phenotypes, and highlights the importance of evaluating  
53 the impact of early-life conditions in the context of an animal's entire life course.

## 54 **INTRODUCTION**

55

56 In humans, the early-life environment exhibits such profound predictive power over  
57 later-life phenotype that the first 1,000 days of life are widely recognized as foundational  
58 for determining future health, quality of life, and even human capital (1). Adverse  
59 conditions in early life can alter brain development (2), dysregulate the immune and  
60 endocrine systems (3, 4), and ultimately increase morbidity and mortality in adulthood  
61 (5). Among nonhuman animals, early-life adversities can exhibit similar far-reaching

62 effects. Challenging ecological conditions during early life are linked to increased adult  
63 parasite load in rabbits (6), inflammation in birds (7), poor reproductive performance in  
64 hyenas (8), and most consistently, reduced lifespan across species (9–11). From an  
65 ecological perspective, a shortened lifespan can result from harsh weather, food  
66 scarcity, or increased competition and predation, which can independently or  
67 collectively cause physiological changes that reduce longevity (e.g., telomere attrition,  
68 (12–14)).

69

70 Beyond ecological challenges, an adverse maternal environment can also reduce  
71 lifespan (15). Juvenile animals can struggle to access maternal resources due to poor  
72 maternal condition, mistimed parturition, or increased rates of sibling competition (16–  
73 19). Such challenges may reduce lifespan as a result of life history trade-offs that  
74 deprioritize developmental systems that promote longevity (18, 20), or, as hypothesized  
75 in humans, by inducing adaptive accelerated reproductive development at the expense  
76 of longevity ((21–23), but see (10)).

77

78 The negative effects of early-life adversity on lifespan are not uni-dimensional, however,  
79 and individuals can be exposed to many forms of early-life adversity simultaneously.  
80 Research has therefore begun to investigate the cumulative influence of multiple early-  
81 life adversities and their varied combinations. These studies reveal that early-life  
82 challenges can combine to collectively reduce longevity (8, 24), fueling an interest in  
83 understanding how animals inhabiting heterogeneous environments may cope with  
84 clusters of adversity during development. Elucidating these patterns can also provide  
85 insight into how animals may respond to the multidimensional environmental shifts  
86 caused by human-induced rapid environmental change (HIREC), which can generate  
87 distinct but co-occurring sources of adversity (25).

88

89 Moreover, some aspects of the future environment may be capable of buffering against  
90 long-term costs of adversity. In highly social animals such as nonhuman primates, the  
91 quality of an individual's social environment predicts longevity (26), and strong social  
92 bonds and high social status during adulthood can ameliorate the negative effects of

93 early-life adversity on survival (27). In solitary animals, the amelioration of early-life  
94 adversity may instead depend on an alternate component of the future environment. For  
95 example, in resource pulse ecosystems where animals experience pronounced  
96 variation in the temporal availability of resources, individuals can be born into food-  
97 scarce environments but subsequently experience a future food boom (28). While this  
98 type of mismatch between the developmental and adult environment has been invoked  
99 to explain the onset of metabolic disease in humans (29, 30), in wild populations, a  
100 resource-rich future environment may free animals from developmental or physiological  
101 constraints created by adverse early-life conditions (18, 31). Thus, if the consequences  
102 of a challenging early environment can be modified by later-life resource access, future  
103 life experience may explain variation in susceptibility to early-life adversity.

104

105 Here, we test the hypothesis that the relationship between early-life adversity on  
106 lifespan can be modified by future food in a population of wild North American red  
107 squirrels (*Tamiasciurus hudsonicus*) inhabiting a resource pulse ecosystem. The  
108 masting cycles of white spruce (*Picea glauca*) trees, red squirrels' preferred food  
109 source, result in food booms (mast years) and busts (non-mast years) that dramatically  
110 impact the availability of spruce cones for squirrels to hoard ahead of winter(32). First,  
111 we identify sources of early-life adversity by determining which environmental  
112 challenges experienced in the first year of life reduce the probability of juvenile survival  
113 (Table 1A). We then examine cumulative effects of early-life adversity on longevity, and  
114 test whether these effects can be ameliorated by later-life resource richness using two  
115 measures of future food availability (Table 1B). We predict that a resource-rich future  
116 will offset, at least in part, the negative effects of early life adversity on lifespan in red  
117 squirrels.

118

119 **Table 1. A) Hypothesized sources of early-life adversity in juvenile squirrels**  
120 **experienced during their first year of life and B) potential resource-related buffers**  
121 **against early-life adversity. References supporting these hypotheses in this study**  
122 **population are provided where available.**

| Variable | Definition | References |
|----------|------------|------------|
|----------|------------|------------|

| <b>A) Early-life adversities</b>                          |  |                  |
|---|--|------------------|
| <i>Large litter size</i>                                  | relatively large number of siblings born within the same litter (increased sibling competition)  | (33)             |
| <i>Litter size mismatched to environmental conditions</i> | litter size is mismatched to future food abundance (e.g., a large litter is produced in a non-mast year when future food is low, a small litter is produced in a mast year when future food is high) | (34, 35)         |
| <i>Later parturition date</i>                             | date of birth is relatively late in the breeding season, resulting in increased conspecific competition for territories  | (36, 37)         |
| <i>Slow postnatal growth rate</i>                         | relatively low offspring growth rate during period of maternal dependence calculated as change in body mass from ~0 d to 25 d of age   | (35, 37, 38)     |
| <i>Non-mast year</i>                                      | a year in which a white spruce mast does not occur and new food production is scarce   | (39)             |
| <i>Elevated squirrel density</i>                          | relatively high number of squirrels living on study area (increased conspecific competition)   | (34, 38, 40, 41) |
| <i>One year following peak in lynx-hare cycle</i>         | a year characterized by a crash in hare density and expected prey-switching by lynx to red squirrels   | (42))            |
| <i>Elevated mustelid density</i>                          | relatively high number of nest predators   | (40, 43)         |
| <i>Extremes in winter temperature</i>                     | relatively warm or cold average winter temperatures  | (40)             |
| <b>B) Potential buffers against early-life adversity</b>  |  |                  |
| <i>Mast year</i>  | encountering a spruce mast event, which results in the production of a superabundance of food, during the second year of life  | (39)             |
| <i>Experimental food supplementation</i>                  | access to a supplemental feeding station at the center of a squirrel's territory   | (44)             |

123 **RESULTS**

124

## 125 **Independent effects of early-life conditions on juvenile survival and lifespan**

126  
127 Six of the 9 potential sources of early-life adversity were negatively associated with  
128 juvenile overwinter survival (Figure 1, Table S1A). Juveniles exhibited poorer overwinter  
129 survival if they were born the year following the peak of the lynx-hare cycle (e.g., when  
130 there is a crash in the snowshoe hare population;  $\beta = -0.76$ ,  $z = -2.28$ ,  $P = 0.022$ ), when  
131 conspecific densities were elevated ( $\beta = -0.51$ ,  $z = -4.25$ ,  $P = 0.000$ ), or when new food  
132 was scarce (i.e., a non-mast year,  $\beta = -1.29$ ,  $z = -4.79$ ,  $P = 0.000$ ). Survival was also  
133 less likely if juveniles grew slowly during the early postnatal period of maternal  
134 dependence (i.e., first 25 days;  $\beta = 0.27$ ,  $z = 4.91$ ,  $P = 0.000$ ), were born later in the  
135 breeding season ( $\beta = -0.25$ ,  $z = -3.5$ ,  $P = 0.001$ ; particularly if conspecific density was  
136 also high,  $\beta = -0.16$ ,  $z = -2.11$ ,  $P = 0.035$ ), were born into a large litter ( $\beta = -0.15$ ,  $z = -$   
137  $2.32$ ,  $P = 0.020$ ) or a litter whose size was mismatched to the environment (e.g., a large  
138 litter in a non-mast year, or a small litter in a mast year;  $\beta = 0.35$ ,  $z = 2.98$ ,  $P = 0.003$ ).  
139 There was no effect of mean overwinter temperature, or mustelid density on juvenile  
140 survival. Males were less likely to survive their first winter than females ( $\beta = -0.76$ ,  $z = -$   
141  $7.83$ ,  $P = 0.000$ , Figure 1A, Table S1A), and had shorter lifespans overall ( $\beta = -0.14$ ,  $z = -$   
142  $-3.18$ ,  $P = 0.001$ , Figure 1B, Table S1B).

143  
144 Only one of the abovementioned factors defined as early-life adversities exhibited  
145 continued, independent effects on total lifespan. Squirrels that were born later in the  
146 breeding season lived shorter lives than those born earlier ( $\beta = -0.07$ ,  $z = -2.68$ ,  $P =$   
147  $0.007$ ; Figure 1B, Table S1B).

## 148 149 **Cumulative effects of early-life adversity on lifespan**

150  
151 Early-life adversity may exhibit divergent effects on longevity and fitness given that  
152 natural selection operates on the latter but not necessarily on the former, so we tested  
153 whether lifespan predicted fitness in our population. We found that lifespan positively  
154 predicted lifetime reproductive success (number of offspring successfully recruited into  
155 the breeding population) in both sexes, such that squirrels that lived longer produced

156 more recruits over their lifetimes than those who died earlier ( $\beta = 2.15$ ,  $z = 14.61$ ,  $P =$   
157  $0.000$ ; Figure S1, Table S2).

158  
159 Most juveniles experienced more than one early-life adversity during the first year of life,  
160 and although only parturition date exhibited continued independent effects on total  
161 lifespan, the sum total of all early-life adversities experienced cumulatively predicted  
162 lifespan ( $\beta = -0.08$ ,  $z = -2.88$ ,  $P = 0.004$ , Figure 2, Table S3). Squirrels experiencing one  
163 adversity lived, on average, 3.1 total years while squirrels experiencing 5 and 6  
164 adversities lived only 2.4 and 2 years, respectively (Figure 2, Table S3).

165  
166 **A high quality future environment mitigates the consequences of early-life**  
167 **adversity**

168  
169 Among squirrels living on the experimental study area, supplementation with a bucket of  
170 peanut butter at the center of their territory increased lifespan ( $\beta = 0.28$ ,  $z = 3.18$   $P =$   
171  $0.001$ ; Figure 3, Table S4). However, we found little evidence that food supplementation  
172 changed the relationship between early-life adversity and lifespan ( $\beta = 0.04$ ,  $z = 0.42$ ,  $P$   
173  $= 0.68$ ). By contrast, experiencing a population-wide food boom in the second year of  
174 life eliminated the negative effects of early-life adversity on lifespan ( $\beta = 0.14$ ,  $z = 2.01$ ,  
175  $P = 0.04$ ; Figure 4, Table S5).

176 **DISCUSSION**

177  
178 A shortened lifespan is a commonly documented consequence of early-life adversity,  
179 reflecting an enduring connection between the early-life environment and end-of-life  
180 outcomes. Here, we show that, in line with prior work in humans and other mammals,  
181 early-life adversities combine to cumulatively reduce lifespan in North American red  
182 squirrels. However, the quality of the future environment modified this relationship.  
183 Future food supplementation increased lifespan for those directly receiving additional  
184 food, but did not influence the relationship between early-life adversity and lifespan.  
185 However, squirrels that experienced a population-wide food boom in their second year  
186 of life did not suffer a shortened lifespan as a result of harsh conditions in their first year

187 of life. Our findings suggest a non-deterministic role of early-life adversity on later-life  
188 phenotype, whereby a high quality future environment can buffer individuals against the  
189 longevity costs associated with challenging early-life conditions.

190

191 Overwinter survival is a key life history stage for juvenile red squirrels as it determines  
192 their recruitment into the breeding population the following spring (40, 45). We found  
193 survival to be lowest among squirrels that were born later in the breeding season, grew  
194 slowly during the postnatal period, or were born into large litters. These patterns reflect  
195 potential challenges related to competition and curtailed maternal investment within the  
196 developmental environment. Later-born squirrels may be less likely to encounter vacant  
197 territories to occupy as many territories will have already been occupied by earlier-born  
198 squirrels. Territory acquisition is critical for overwinter survival (40), thus later-born  
199 squirrels face increased conspecific competition for territories and in turn, higher rates  
200 of early mortality (33). Similarly, sibling competition for maternal resources is largest in  
201 large litters. Such competition manifests as a quantity/quality trade-off in which pups  
202 born into larger litters exhibit slower growth (46), which reduces a squirrel's ability to  
203 compete for its own natal territory as well as territories adjacent to it (33).

204

205 Beyond the maternal environment, juvenile mortality was predicted by harsh ecological  
206 conditions, including predation risk by Canada lynx, which exhibit prey-switching from  
207 snowshoe hares to red squirrels in years after hare populations crash (42, 47). Squirrels  
208 born in the year following a hare crash are therefore at the highest risk of predation and  
209 more likely to suffer direct predation events by lynx. In addition, elevated squirrel  
210 densities (which increase conspecific competition for both food and territories) and food  
211 scarcity were additional ecological sources of early-life mortality. In line with prior work,  
212 juveniles born in non-mast years when new food is scarce were less likely to survive  
213 (34), particularly when maternal reproductive effort was mismatched to the environment  
214 such that sibling and conspecific competition was high when food was low (e.g., a large  
215 litter in a low food (non-mast) year; (35)).

216



217 Similar to correlations between socioeconomic status, educational attainment, and  
218 health in humans, environmental covariance can generate clusters of adversity in which  
219 multiple ecological challenges co-occur (48). Though only parturition date exhibited  
220 continued, independent effects on lifespan, all sources of early-life adversities predicted  
221 lifespan when considered cumulatively, illustrating the need to consider that early-life  
222 challenges alone may not explain variation in lifespan until they compound with other  
223 simultaneous challenges. Most squirrels experienced at least 1 source of early-life  
224 adversity, and the consequences of harsh early-life conditions for lifespan increased  
225 with increasing numbers of early-life adversities. This pattern echoes previous work in  
226 both humans and nonhuman animals indicating that clusters of early life adversity may  
227 be particularly prevalent in populations inhabiting highly fluctuating environments and/or  
228 environments in which multiple sources of early-life adversity are expected to coincide  
229 (8, 24).

230  
231 Human research has long endeavored to explain how the biological embedding of early-  
232 life adversity leads to variation in individual health and longevity (49, 50). What remains  
233 largely unknown are what, if any, factors can buffer against such embedding. Moreover,  
234 if the negative effects of harsh early environments are non-deterministic such that they  
235 can be mitigated by other factors like a high quality later-life environment, then  
236 consideration of an individual's entire life course is essential to explaining variation in  
237 susceptibility to early-life adversity. We found that squirrels that received a  
238 supplemental food bucket on their territories lived longer than those that did not, but the  
239 relationship between early-life adversity and longevity was unaffected by food  
240 supplementation. By contrast, squirrels that experienced a population-wide food boom  
241 (i.e., "mast year") in their second year of life did not suffer reduced lifespans as a result  
242 of early-life adversity. Although they occur episodically, the boom of food produced in  
243 mast years serves as a catapult for Darwinian fitness in red squirrels, increasing both  
244 annual and lifetime reproductive success (34, 35). Our results suggest that mast events  
245 can also alleviate the longevity costs of harsh early-life conditions, potentially by  
246 relieving energetic constraints at the population level and thus increasing environmental  
247 quality and reducing food competition for the entire population of squirrels.

248

249 These results extend our current understanding of the role of early life effects on later-  
250 life phenotype by uncovering one dimension of the future environment, population-wide  
251 resource availability, that can buffer against the negative effects of early-life adversity  
252 on lifespan. Although food booms and their effects may be unique to resource pulse  
253 ecosystems, they reflect dramatic increases in environmental quality that benefit entire  
254 populations, and serve as natural experiments that mimic large-scale environmental  
255 perturbations (28). Beyond enhancing Darwinian fitness, we show that population-wide  
256 food booms alter expected relationships between early-life environments and later-life  
257 phenotype, and possibly patterns of senescence, in ways that providing individuals with  
258 supplemental food cannot. Inter-individual variation in vulnerability and resilience to  
259 early-life adversity may therefore hinge on changes in larger-scale patterns of  
260 competition and constraint in which individual benefits to longevity and fitness hinge on  
261 benefits conferred to the entire population.

## 262 **MATERIALS AND METHODS**

### 263 *Study system*

264 We have studied North American red squirrels (*Tamiasciurus hudsonicus*) in the  
265 southwestern Yukon, Canada (61°N, 138°W) since 1989 (32). Detailed information  
266 about the study system and field methods can be found elsewhere (32, 45). Briefly, we  
267 followed squirrels from birth until death on two separate ~40 hectare study areas (Kloo  
268 or “KL” and Sulphur or “SU”) as well as an experimental study area (Agnes or “AG”),  
269 identifying individual squirrels using uniquely labeled metal ear tags placed shortly after  
270 birth while still in their natal nest or at first capture during regular live-trapping. We  
271 censused the entire population in May and August or September of each year. Because  
272 red squirrels are highly territorial and trappable, our detection probability does not differ  
273 from 1 and a lack of detection during a census is indicative of death (51). This enables  
274 us to confidently estimate lifespan (median = 3.5 y, maximum = 9 y; (45)).

275

### 276 *Life-history and fitness data*

277 We determined female reproductive status via abdominal palpation for fetus  
278 development and by monitoring individual mass gain during regular live-trapping. Within

279 a few days of birth, we located each nest using radio-telemetry, counted, ear clipped  
280 (for unique marking within each litter and tissue sample), and weighed each pup (to the  
281 nearest tenth of a gram). About 25 days later, we reweighed each pup and affixed a set  
282 of permanent metal ear tags. Because growth is linear during this period of  
283 development (37), we calculated pup postnatal growth rate as the mass gain per day.  
284 To calculate lifetime reproductive success, we summed the number of recruits produced  
285 by each squirrel over their lifetime. We determined the sire of each pup produced by  
286 analyzing tissue samples, assigning loci with GENEMAPPER software 3.5 (Applied  
287 Biosystems), and assigning paternity with CERVUS v.3.0 with 99% confidence (52, 53).  
288 Details on microsatellite loci isolation and paternity assignment can be found in prior  
289 studies (54–56). We considered a pup as recruited into the breeding population if they  
290 survived to 200 days old (37, 57, 58).

291

#### 292 *Temperature data*

293 We used daily temperature records from the Haines Junction weather station, which is  
294 located ~35 km SE from our study area (Climate ID 2100630, 60.77°N, 137.57°W), to  
295 calculate yearly mean overwinter temperatures from the months of October to the  
296 following March. Prior studies in our population using data from this weather station  
297 demonstrate that mean overwinter temperatures capture thermoregulatory costs of  
298 temperature extremes and impact juvenile survival and litter failure (40, 43).

299

#### 300 *Predator data*

301 We used data on two predators of juvenile red squirrels from our study area, Canada  
302 lynx (*Lynx canadensis*) and mustelids (short-tailed weasel *Musela erminea*, least  
303 weasel *M. nivalis*, and marten *Martes americana*), from the Kluane Boreal Forest  
304 Ecosystem Project (1987-1996) and the Community Ecological Monitoring Program  
305 (1996-present). Lynx and mustelid densities were calculated as the average snow track  
306 count per 100 kilometer transect (59). We also calculated the density of snowshoe  
307 hares (*Lepus americanus*), on which Canada lynx specialize, using mark-recapture (59)  
308 because lynx prey-switch to red squirrels following crashes in hare population densities  
309 (47). Following prior studies (42), we binned the hare-lynx cycle into 4 categories based  
310 on the location in the cycle: peak hare density (when both hare and lynx density are

311 high), 1-year post hare peak (when hare density crashes, but lynx density remains  
312 high), 2-years post peak (when lynx density crashes), and any other year in the cycle.  
313 Low juvenile recruitment suggests red squirrel predation risk from lynx is highest 1-year  
314 post hare peak (42).

315

### 316 *Measures of food availability*

317 Food boom. Each year, we counted the number of visible cones on one side of the top 3  
318 meters of a consistent subset of trees (between 159-254 trees) on each study area (60).  
319 We then log (+1) transformed counts and calculated the mean to represent an annual  
320 index (61). We then defined years with a superabundance of cones as mast years,  
321 which occur once every 3-7 years (34).

322

323 Experimental food supplementation. From 2005-2017 except for years following the  
324 2010 and 2014 masts, we experimentally supplemented a subset of squirrels living on a  
325 separate study area (AG) by hanging a bucket containing 1 kg of peanut butter between  
326 two trees at the center of the supplemented squirrel's territory. We replenished peanut  
327 butter approximately every 6 weeks from October to May and replenished peanut butter  
328 to any lactating females through the summer months. One kg of peanut butter is  
329 approximately equal to the resting metabolic needs of an individual for 70 days (62, 63).

330

### 331 *Statistical analysis*

332 We conducted all analyses in R version 4.0.2. We used the package *lme4* to conduct  
333 generalized linear mixed models (GLMM) and the package *visreg* to visualize partial  
334 regressions. We controlled for study area (fixed effect), litter number (fixed effect), litter  
335 identity (random effect), and year (random effect) in all models. Some models also  
336 contained mother identity as an additional random effect if the model would converge  
337 with this additional structure.

338

339 We defined early-life factors as early-life adversities if they significantly reduced the  
340 likelihood of juvenile survival using a set of 9 putative early-life adversities assembled  
341 based on prior work in our study population (Table 1). To do this, we constructed a  
342 model to test which of these factors experienced during a squirrel's birth year were

343 related to survival over a squirrel's first winter to the following May (i.e., spring census)  
344 using a binary error distribution (survived yes/no). We used pup growth rate, litter size  
345 (number of pups), parturition date (day-of-year), mast year (yes/no), year in the hare-  
346 lynx cycle (hare peak, 1-year post peak, 2-years post peak, other), squirrel population  
347 density, mustelid density, and mean winter temperature (see rationale for these  
348 predictions in Table 1). We also included interactions of litter size x mast, parturition  
349 date x squirrel density, and pup growth rate x squirrel density as predictors as the  
350 effects of these factors on juvenile survival may be dependent on other co-occurring  
351 variables (e.g., being born late in the year may only have a negative effect if conspecific  
352 competition that year is high, etc.).

353  
354 We next confirmed that lifespan was a fitness-relevant trait by testing whether the total  
355 number of recruits produced during a squirrel's life (response) was related to lifespan (#  
356 of years), sex, and their interaction as predictors using a GLMM with Poisson  
357 distribution. To determine if early-life adversities exerted continued, independent effects  
358 on lifespan beyond the juvenile period, we ran an identical model to the one described  
359 above except we used lifespan (i.e. longevity conditional upon survival to 200 days) as  
360 the dependent variable rather than juvenile survival. We then tested whether early-life  
361 adversities exhibited cumulative effects on lifespan. To do this, we summed the total  
362 number of early-life adversities (1 = exposed, 0 = not exposed) that each squirrel  
363 experienced. For continuous variables, we binned data into the lower or upper half of  
364 the distribution, determined which bin reduced juvenile survival, and assigned this bin  
365 as an adversity (e.g., if the upper half of the distribution of conspecific density reduced  
366 juvenile survival, then squirrels experiencing densities in that upper bin were considered  
367 to be exposed to adversity and thus assigned "1"). We then ran another GLMM  
368 (Poisson) examining the relationship between the cumulative number of early life  
369 adversities (fixed effect) and lifespan (response). We confirmed this effect was linear by  
370 additionally testing for quadratic ( $z = -1$ ,  $p = 0.921$ ) and cubic ( $z = 0.5$ ,  $p = 0.603$ ) terms  
371 and fitting splines with general additive models.

372

373 Finally, we tested whether future resources (a future food boom and experimental  
374 supplementation with peanut butter) ameliorated the cost of early-life adversities on  
375 lifespan (i.e., # of early-life adversities x resource). First, we tested whether  
376 experimental supplementation with *ad libitum* peanut butter ameliorated costs of early-  
377 life adversity. We restricted this analysis to cohorts born between 2004-2015 to focus on  
378 cohorts that had the potential to live at least 4 years before monitoring ended on the  
379 experimental grid in 2019. Squirrels (N = 263 individuals, 10 cohorts) either received a  
380 bucket of peanut butter on their territory or did not (binary variable). Then, we ran a  
381 model in which we added an interaction of early-life adversity with whether an individual  
382 encountered a spruce mast during its second year of life.

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### 392 **FIGURE LEGENDS**

393  
394 **Fig 1. Harsh conditions in the first year of life independently predict poor**  
395 **overwinter survival and reduced lifespan. (A)** Six of the 9 potential early-life  
396 adversities were associated with a reduced likelihood of juvenile overwinter survival  
397 (i.e., survival past the first 200 d). **(B)** Parturition date was the only early-life adversity to  
398 demonstrate a continued effect on lifespan for those individuals that survived their first  
399 winter. Forest plots depict results of generalized linear mixed-effects model testing  
400 which early-life factors predict juvenile overwinter survival (N = 3,699 squirrels) and  
401 lifespan (N = 886 squirrels). Purple bars denote factors that significantly ( $P > 0.05$ )

402 negatively correlate with survival; green bars denote factors that significantly positively  
403 correlate with survival; gray bars denote non-significant factors.

404

405 **Fig 2. Early-life adversities cumulatively reduce longevity.** Although only two early-  
406 life factors significantly independently associated with lifespan, squirrels that  
407 experienced multiple adversities identified as reducing juvenile overwinter survival  
408 (Figure 1) exhibited shorter lifespans. Partial residual plot depicts the relationship  
409 between the number of early-life adversities experienced and lifespan (N = 886  
410 squirrels).

411

412 **Figure 3. Experimental food supplementation extends lifespan but does not**  
413 **change the relationship between early-life adversity and lifespan.** Scatterplot  
414 depicts partial residuals from a generalized linear-mixed effects model testing whether  
415 providing individual squirrels with *ad libitum* peanut butter at the center of their territories  
416 could ameliorate the negative effects of early-life adversity on lifespan (N = 263  
417 squirrels).

418

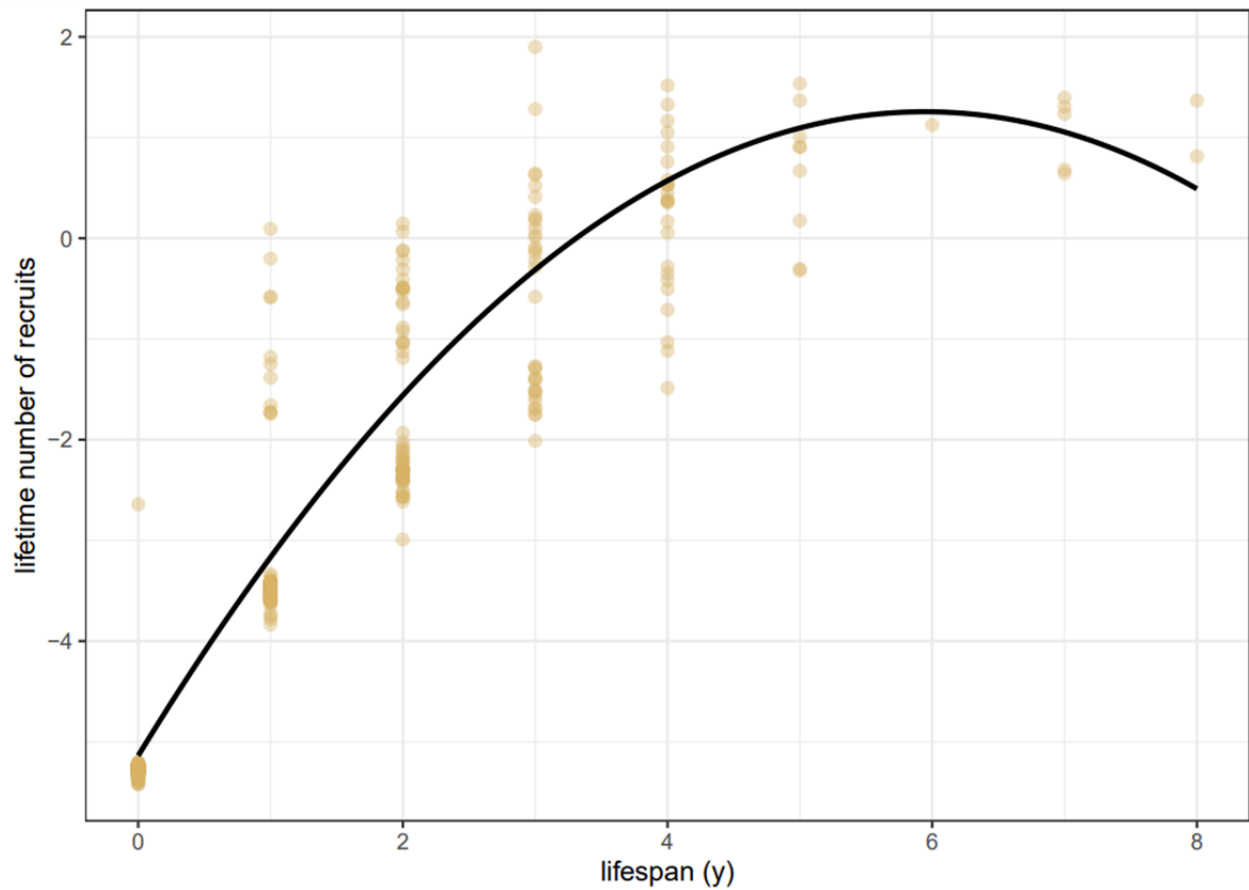
419 **Figure 4. A future food boom eliminates the negative effects of early-life adversity**  
420 **on lifespan.** Squirrels that experienced multiple adversities but encountered a spruce  
421 mast event during their second year of life did not suffer shortened lifespans despite  
422 multiple adversities. Scatterplot depicts partial residuals from a generalized linear  
423 mixed-effects model testing whether encountering a food boom (mast year) in the  
424 second year of life (yes/no) modified the relationship between cumulative early-life  
425 adversities and longevity (N = 886 squirrels).

426 **SUPPLEMENTARY MATERIALS**

427 **Figures**

428

429 **Figure S1. Lifespan positively predicts lifetime reproductive success in Yukon red**  
430 **squirrels.** Among both male and female squirrels, longer lives were associated with  
431 more offspring successfully recruited into the breeding population over the lifetime  
432 (lifetime reproductive success; N = 1,197 squirrels). Scatterplot depicts partial residuals  
433 from a generalized linear mixed-effects model.  
434



435



436 **Tables**

437

438 **Table S1. Harsh early-life conditions independently predict reduced juvenile**  
 439 **survival, with limited independent effects on lifespan.** A) Juvenile squirrels were  
 440 more likely to die overwinter (i.e., the first 200 days of life) if they were male, born into  
 441 large litters, born later in the breeding season, grew slowly during the first 25 days  
 442 postnatal of life, it was a low food (i.e., non-mast) year, squirrel densities were high, or it  
 443 was the year following a crash in the snowshoe hare population (more likely to  
 444 experience prey-switching by lynx to squirrels). Squirrels born into large litters in non-  
 445 mast years (litter size x mast interaction) or late in the breeding season in high density  
 446 years (squirrel density x parturition date) also exhibited a smaller likelihood of  
 447 overwinter survival. B) Only sex and parturition date were independently associated with  
 448 total lifespan, such that squirrels born male or later in the breeding season lived shorter  
 449 lives. There was a trend toward shorter lifespans for squirrels born in high squirrel  
 450 density years or in the year following a hare crash. Analysis of lifespan was restricted to  
 451 squirrels that survived through their first winter (i.e., to adulthood). Results reflect output  
 452 from generalized linear mixed-effects models. Continuous predictors were centered to a  
 453 mean of zero and expressed in standard deviations.

454

| Independent terms                       | (A) Juvenile survival (N = 3,736) |             |              |              | (B) Adult lifespan (N = 913) |             |              |              |
|---|-----------------------------------|-------------|--------------|--------------|------------------------------|-------------|--------------|--------------|
|   | Estimate                          | SE          | Z            | P            | Estimate                     | SE          | Z            | P            |
| <b>intercept</b>                        | <b>-1.30</b>                      | <b>0.16</b> | <b>-8.13</b> | <b>0.000</b> | <b>1.03</b>                  | <b>0.06</b> | <b>17.46</b> | <b>0.000</b> |
| grid (SU)                               | 0.05                              | 0.11        | 0.43         | 0.670        | -0.03                        | 0.05        | -0.62        | 0.533        |
| <b>sex (male)</b>                       | <b>-0.76</b>                      | <b>0.10</b> | <b>-7.83</b> | <b>0.000</b> | <b>-0.14</b>                 | <b>0.04</b> | <b>-3.18</b> | <b>0.001</b> |
| <b>litter size</b>                      | <b>-0.15</b>                      | <b>0.07</b> | <b>-2.32</b> | <b>0.020</b> | 0.01                         | 0.03        | 0.17         | 0.865        |
| <b>parturition date</b>                 | <b>-0.26</b>                      | <b>0.06</b> | <b>-4.50</b> | <b>0.000</b> | <b>-0.07</b>                 | <b>0.02</b> | <b>-2.68</b> | <b>0.007</b> |
| <b>growth rate</b>                      | <b>0.27</b>                       | <b>0.06</b> | <b>4.91</b>  | <b>0.000</b> | 0.02                         | 0.02        | 0.74         | 0.458        |
| <b>mast (no)</b>                        | <b>-1.29</b>                      | <b>0.27</b> | <b>-4.79</b> | <b>0.000</b> | 0.11                         | 0.09        | 1.20         | 0.231        |
| <b>squirrel density</b>                 | <b>-0.51</b>                      | <b>0.12</b> | <b>-4.25</b> | <b>0.000</b> | -0.07                        | 0.04        | -1.81        | 0.071        |
| lynx-hare cycle (peak)                  | 0.22                              | 0.32        | 0.70         | 0.482        | -0.13                        | 0.12        | -1.12        | 0.262        |
| <b>lynx-hare cycle (1-yr post peak)</b> | <b>-0.76</b>                      | <b>0.33</b> | <b>-2.28</b> | <b>0.022</b> | -0.27                        | 0.14        | -1.91        | 0.056        |
| lynx-hare cycle (2-yrs post peak)       | -0.33                             | 0.33        | -0.99        | 0.321        | -0.07                        | 0.12        | -0.55        | 0.585        |

|  |              |             |              |                 |       |      |       |                 |
|--|--------------|-------------|--------------|-----------------|-------|------|-------|-----------------|
| mustelid density                           | 0.06         | 0.11        | 0.58         | 0.559           | 0.03  | 0.04 | 0.72  | 0.473           |
| mean winter temperature                    | -0.03        | 0.11        | -0.25        | 0.800           | -0.05 | 0.04 | -1.33 | 0.183           |
| <b>litter size x mast (yes)</b>            | <b>0.35</b>  | <b>0.12</b> | <b>2.98</b>  | <b>0.003</b>    | -0.02 | 0.05 | -0.42 | 0.675           |
| <b>parturition date x squirrel density</b> | <b>-0.16</b> | <b>0.08</b> | <b>-2.11</b> | <b>0.035</b>    | 0.00  | 0.03 | 0.05  | 0.961           |
| growth rate x squirrel density             | -0.09        | 0.07        | -1.43        | 0.153           | 0.02  | 0.02 | 0.67  | 0.503           |
| <b>random effects</b>                      |              |             |              | <b>std.</b>     |       |      |       | <b>std.</b>     |
|  |              |             |              | <b>variance</b> |       |      |       | <b>variance</b> |
|  |              |             |              | <b>dev.</b>     |       |      |       | <b>dev.</b>     |
| litter identity                            |              |             | 0.76         | 0.87            |       | 0.01 |       | 0.12            |
| maternal identity                          |              |             | 0.00         | 0.00            |       | 0.02 |       | 0.14            |
| cohort                                     |              |             | 0.21         | 0.46            |       | 0.02 |       | 0.14            |

455

456 **Table S2. Lifespan is positively correlated with lifetime reproductive success in**  
457 **red squirrels.** Squirrels that lived longer lives also successfully recruited more pups  
458 into the breeding population (lifetime reproductive success). Results reflect output from  
459 a generalized linear mixed-effects model. A non-significant interaction between sex and  
460 lifespan was removed to construct the final model below.

| Independent terms     | Lifetime reproductive success (N = 1,197) |      |                 |                  |
|-----------------------|---|------|-----------------|------------------|
|                       | Estimate                                  | SE   | Z               | P                |
| intercept             | -4.5                                      | 0.32 | -14.15          | 0.000            |
| lifespan              | 2.15                                      | 0.15 | 14.61           | 0.000            |
| lifespan (quadratic)  | -0.18                                     | 0.02 | -10.17          | 0.000            |
| sex(male)             | -0.63                                     | 0.21 | -2.93           | 0.000            |
| <b>random effects</b> |   |      | <b>variance</b> | <b>std. dev.</b> |
| litter identity       |   |      | 0.61            | 0.78             |
| cohort                |   |      | 0.06            | 0.24             |

461

462 **Table S3. The number of early-life adversities experienced in the first year of life**  
463 **cumulatively predict lifespan.** The more co-occurring, independent early-life  
464 adversities a squirrel experienced in their first year of life, the shorter their total lifespan.  
465 Results depict output from generalized linear mixed-effects model; number of  
466 adversities were scaled to a mean of zero and expressed in standard deviations.

| Independent terms          | Lifespan (N = 886) |             |                 |                  |
|----------------------------|--------------------|-------------|-----------------|------------------|
|                            | Estimate           | SE          | Z               | P                |
| <b>intercept</b>           | <b>1.02</b>        | <b>0.05</b> | <b>20.31</b>    | <b>0.000</b>     |
| <b># adversities</b>       | <b>-0.08</b>       | <b>0.03</b> | <b>-2.88</b>    | <b>0.004</b>     |
| grid (SU)                  | -0.04              | 0.05        | -0.94           | 0.346            |
| <b>sex (male)</b>          | <b>-0.14</b>       | <b>0.04</b> | <b>-3.21</b>    | <b>0.001</b>     |
| # adversities * sex (male) | -0.02              | 0.04        | -0.37           | 0.712            |
| <b>random effects</b>      |                    |             | <b>variance</b> | <b>std. dev.</b> |
| litter identity            |                    |             | 0.02            | 0.14             |
| maternal identity          |                    |             | 0.02            | 0.13             |
| cohort                     |                    |             | 0.03            | 0.17             |

467

468 **Table S4. Individual supplementation with peanut butter increases lifespan but**  
469 **does not alter the relationship between early-life adversity and longevity.** On a  
470 separate experimental study grid, a subset of squirrels received a bucket of peanut  
471 butter at the center of their territory. Squirrels that received a bucket on their territory  
472 lived longer than those that did not, but the negative relationship between early-life  
473 adversities and lifespan remained was not modified by whether a squirrel received a  
474 supplemental food bucket. Results depict output from a generalized linear mixed-effects  
475 model. Early-life adversities were scaled to a mean of zero and expressed in standard  
476 deviations.

| Independent terms            | Lifespan (N = 263) |             |                 |                  |
|------------------------------|--------------------|-------------|-----------------|------------------|
|                              | Estimate           | SE          | Z               | P                |
| litter number (second)       | -0.04              | 0.12        | -0.36           | 0.722            |
| sex (male)                   | -0.09              | 0.08        | -1.11           | 0.264            |
| # adversities                | 0.04               | 0.09        | 0.51            | 0.613            |
| <b>bucket (yes)</b>          | <b>0.28</b>        | <b>0.09</b> | <b>3.18</b>     | <b>0.001</b>     |
| # adversities x bucket (yes) | 0.04               | 0.09        | 0.42            | 0.677            |
| <b>random effects</b>        |                    |             | <b>variance</b> | <b>std. dev.</b> |
| cohort                       |                    |             | 0.02            | 0.14             |

477

478

479 **Table S5. A food boom experienced in the second year of life rescues the**  
480 **negative effects of early-life adversity on lifespan.** Regardless of how many early-  
481 life adversities a squirrel experienced in their first year of life, they did not suffer a  
482 shortened lifespan if they experienced a food boom (mast year) in their second year of  
483 life. Results depict output from a generalized linear mixed-effects model. Number of  
484 adversities were scaled to a mean of zero and expressed in standard deviations.

| Independent terms                        | Lifespan (N = 886) |             |                 |                  |
|--|--------------------|-------------|-----------------|------------------|
|  | Estimate           | SE          | Z               | P                |
| <b>intercept</b>                         | <b>1.03</b>        | <b>0.05</b> | <b>19.35</b>    | <b>0.000</b>     |
| <b># adversities</b>                     | <b>-0.10</b>       | <b>0.03</b> | <b>-3.42</b>    | <b>0.000</b>     |
| <b># adversities x year 2 mast (yes)</b> | <b>0.14</b>        | <b>0.07</b> | <b>2.01</b>     | <b>0.044</b>     |
| year 2 mast (yes)                        | -0.08              | 0.11        | -0.78           | 0.437            |
| grid (SU)                                | -0.04              | 0.05        | -0.79           | 0.427            |
| <b>sex (male)</b>                        | <b>-0.14</b>       | <b>0.04</b> | <b>-3.30</b>    | <b>0.001</b>     |
| <b>random effects</b>                    |                    |             | <b>variance</b> | <b>std. dev.</b> |
| litter identity                          |                    |             | 0.02            | 0.14             |
| maternal identity                        |                    |             | 0.01            | 0.12             |
| cohort                                   |                    |             | 0.03            | 0.17             |

485

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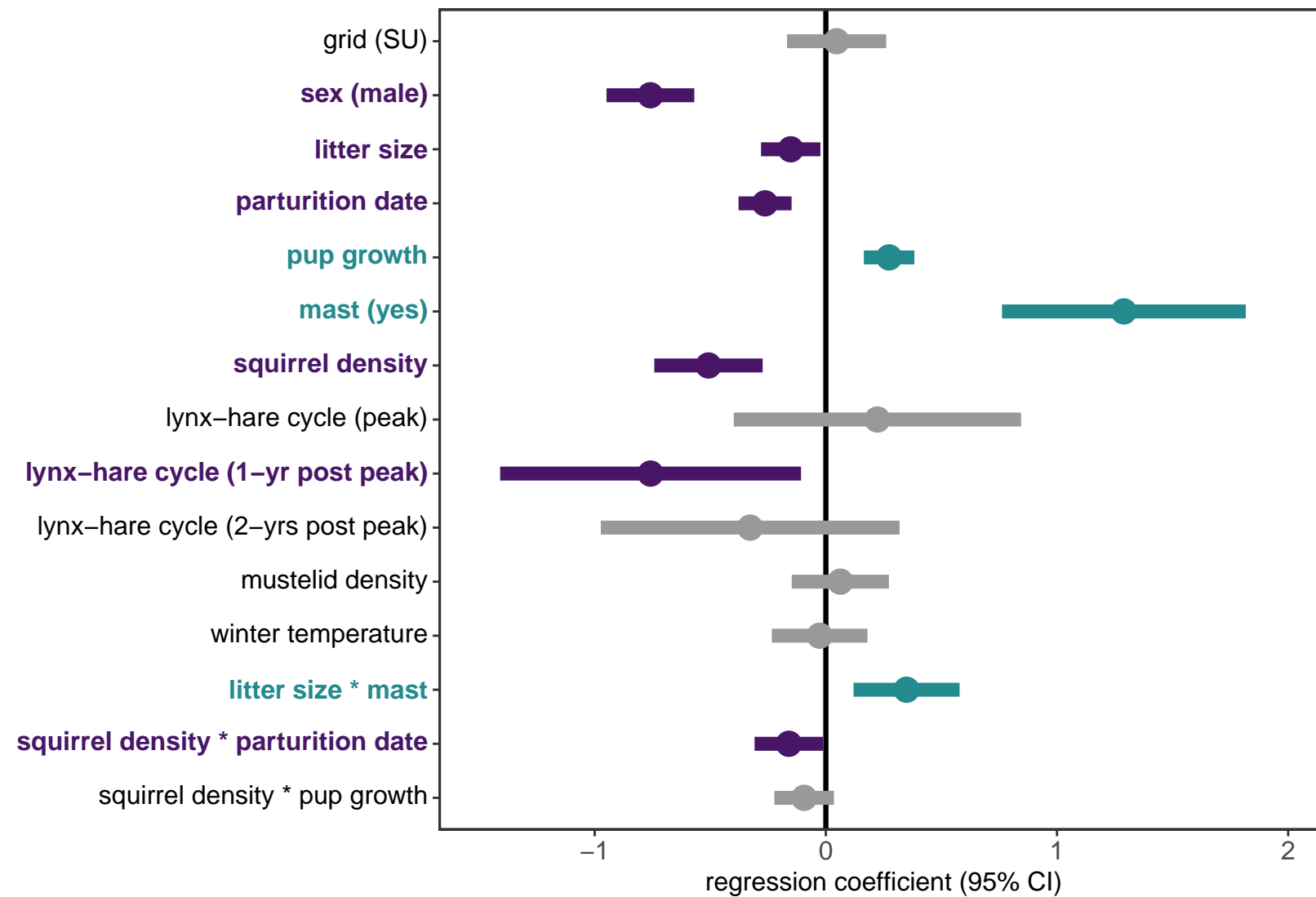
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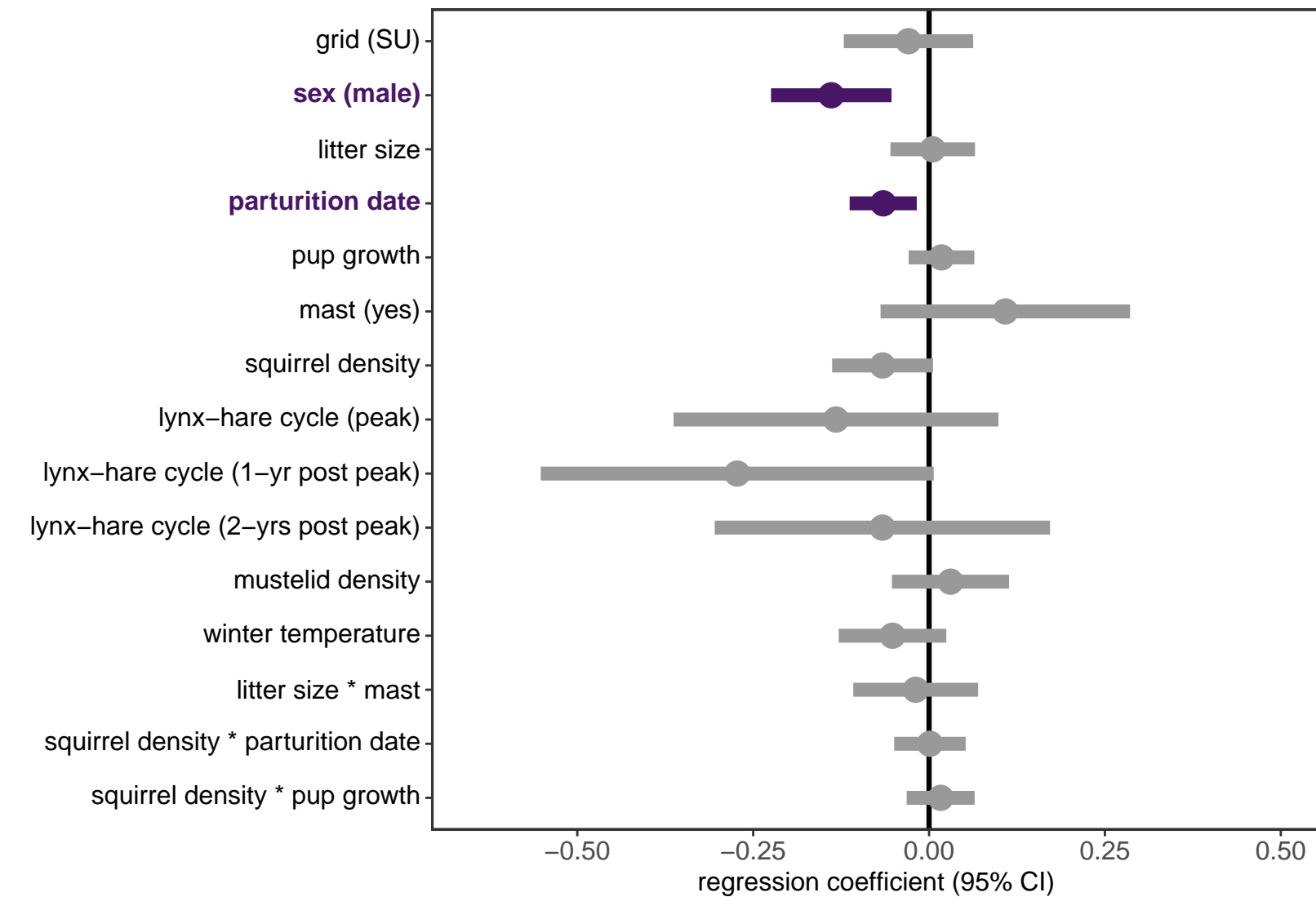
A

## juvenile overwinter survival

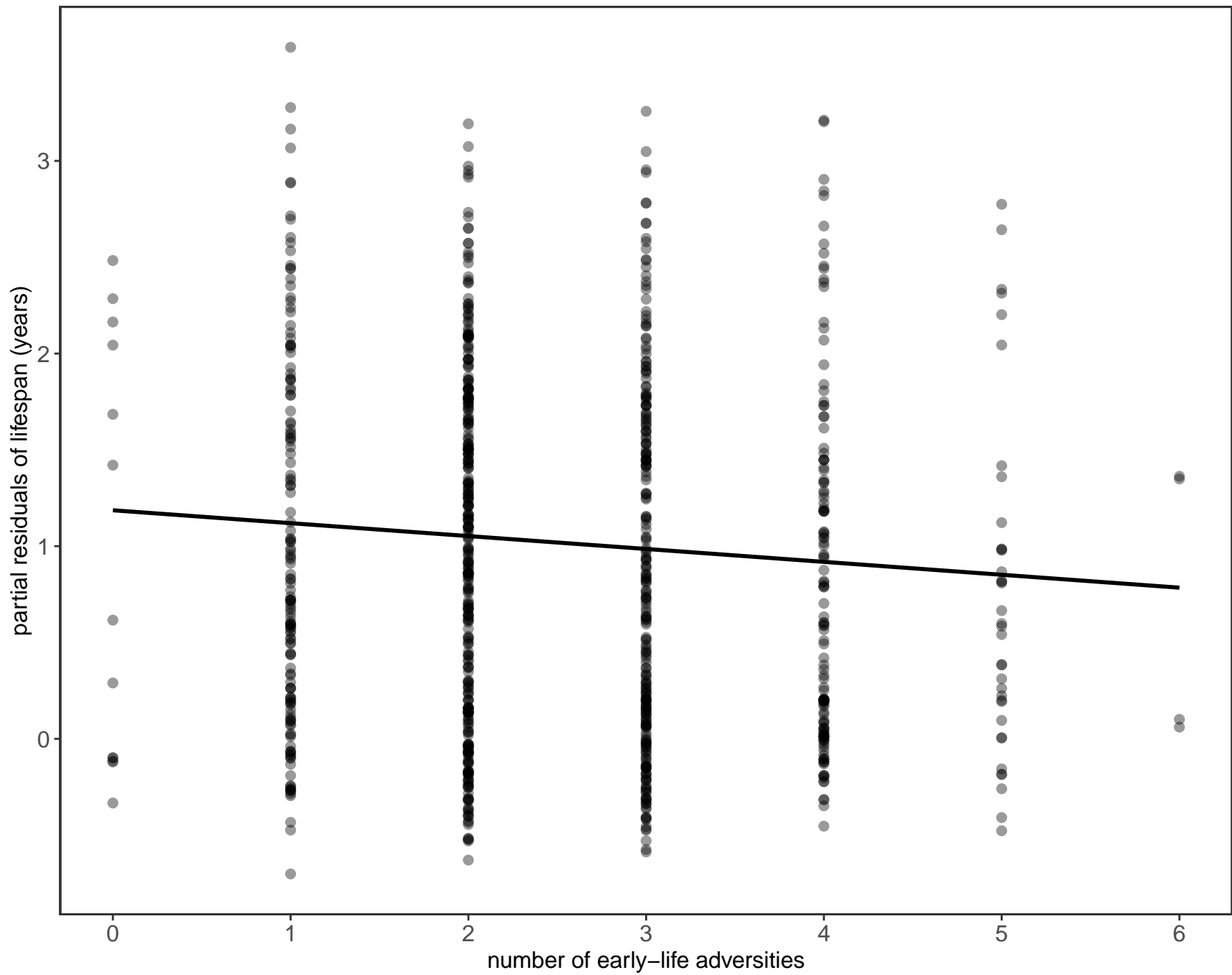


B

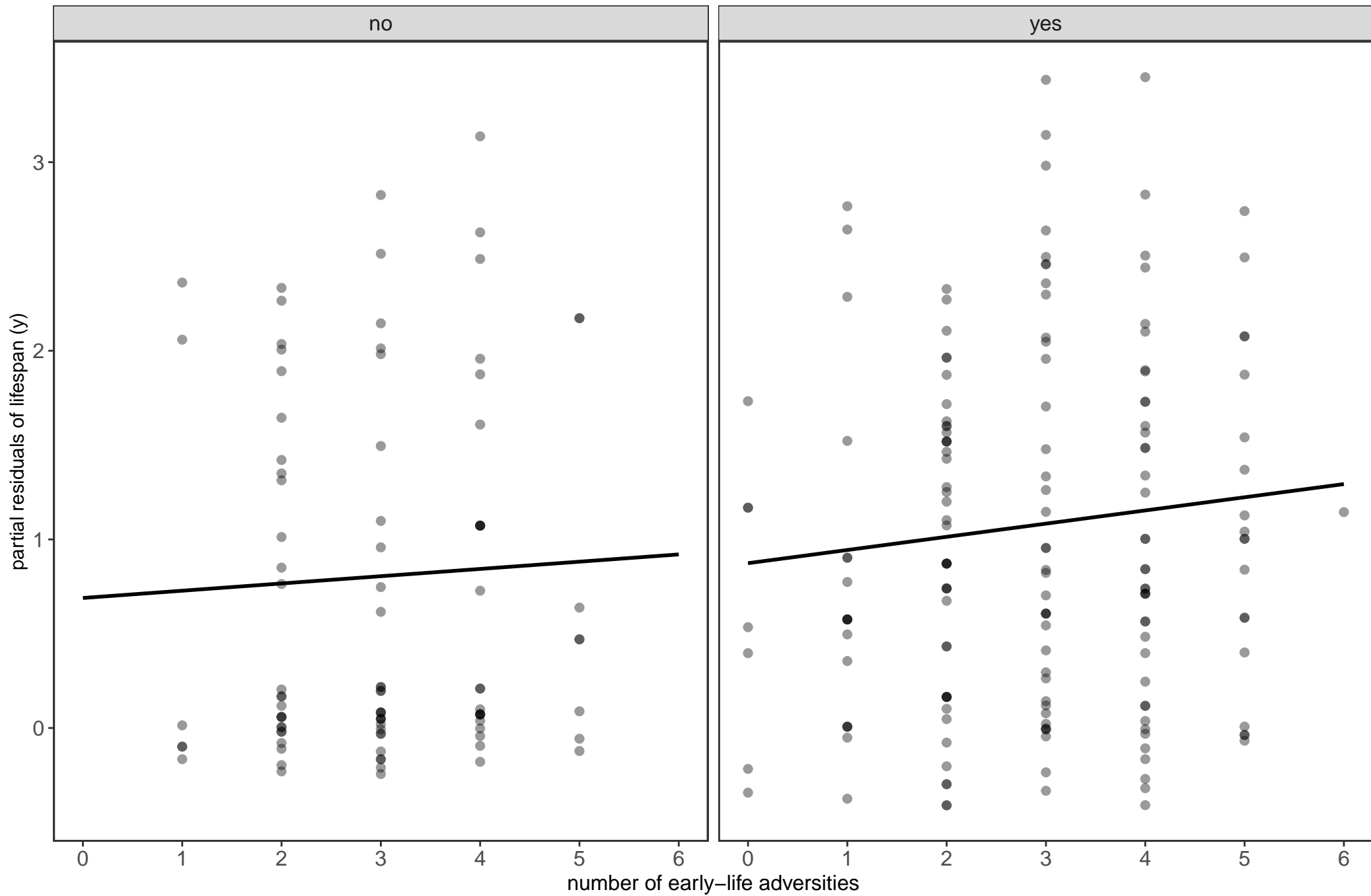
## lifespan



# cumulative effects of early-life adversity



# experimental food supplementation



# encountering a food boom in second year of life

