Individual differences in developmental trajectory leave a male polyphenic signature in bulb mite populations

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Abstract

Developmental plasticity alters phenotypes and can in that way change the response to selection. When alternative phenotypes show different life history trajectories, developmental plasticity can also affect, and be affected by, population size-structure in an eco-evolutionary interaction. Developmental plasticity often functions to anticipate future conditions but it can also mitigate current stress conditions. Both types of developmental plasticity have evolved under different selections and this raises the question if they underlie different eco-evolutionary population dynamics. Here, we tested, in a long-term population experiment using the male polyphenic bulb mite (*Rhizoglyphus robini*), if the selective harvesting of juveniles of different developmental stages concurrently alters population size (ecological response) and male adult phenotype expression (evolutionary response) in line with eco-evolutionary predictions that assume the male polyphenism is anticipatory or mitigating. We found that the frequency of adult males that expressed costly (fighter) morphology was lowest under the most severe juvenile harvesting conditions. This response cannot be explained if we assume that adult male phenotype expression is to anticipate adult (mating) conditions because, in that case, only the manipulation of adult performance would have an effect. Instead, we suggest that juveniles mitigate their increased mortality risk by expediating ontogeny to forego the development of costly morphology and mature quicker but as a defenceless scrambler. If, like in mammals and birds where early-life stress effects are extensively studied, we account for such pre-adult viability selection in coldblooded species, it would allow us to (i) better characterise natural selection on trait development like male polyphenisms, (ii) understand how it can affect the response to other selections in adulthood, and (iii) understand how such trait dynamics influence, and are influenced by, population dynamics.

Keywords: alternative male phenotypes, dispersal, eco-evolutionary dynamics, male morph coexistence, polyphenism

Introduction

Across the animal kingdom, developmental plasticity comprises a switch to alternative developmental pathways that depends on an individual's condition – the resource budget available for the production and maintenance of adaptive traits (Hill 2011; Casasa et al. 2020; Nijhout & McKenna 2018) – and which can lead to food-dependent allometric plasticity and the adaptive expression of alternative phenotypes in adulthood (polyphenism) (West-Eberhard 2003; Nijhout & McKenna 2018). For example, many intraspecific, arthropod male dimorphisms comprise large majors that have weapons for male-male competition, and smaller, weaponless minors that sneak matings (Moczek 2003; Smallegange 2011; Buzatto & Machado 2014). Importantly, these adaptive, condition-dependent alternative phenotypes typically have different survival, growth and reproduction rates because they follow different developmental trajectories (West-Eberhard 2003; Smallegange 2011; Weir et al. 2016). Differences in individual development, be they plastic or genetic, will thus affect a population's structure, size and growth. Such population changes can in turn influence individual development through processes like density-dependent competition over resources (food) and density-dependent selection (Travis et al. 2013), creating eco-evolutionary feedbacks at the population level (Smallegange & Deere 2014; Croll et al. 2019; Smallegange 2022). However, accurately predicting the population dynamical responses to perturbation of developmental trajectories is still difficult (Smallegange et al. 2019; Smallegange 2022).

The way in which a perturbation to individual development can impact the eco-evolutionary dynamics of populations depends on what selection pressures are assumed to act on adaptive developmental plasticity (Smallegange 2022). Different selection pressures determine different types of adaptive developmental plasticity (e.g., Forsman 2015; Nettle and Bateson 2015) and here we focus on two distinct types: anticipatory and mitigating adaptive developmental plasticity (Smallegange et al. 2019; Smallegange 2022). Specifically, in case of the minor and major males described above, whether a male develops into an armed major male or an unarmed minor male depends on whether it reaches a critical resource budget threshold, assumed to be approximated by

52 a body size threshold, during development (Plaistow et al. 2005; Sasson et al. 2016; Cotton et al.
53 2004). If the adaptive developmental plasticity is *anticipatory*, this condition-cued threshold
54 mechanism can be interpreted as the evolutionary result of disruptive sexual selection on alternative
55 mating tactics (West-Eberhard 2003; Smallegange et al. 2019): good-condition juvenile males
56 maximise fitness by becoming majors, anticipating competitive mating success; bad-condition
57 juveniles anticipate failure at competitive success and salvage fitness by becoming minors (Shuster &
58 Wade 2003). On the other hand, the condition-cued threshold mechanism could be part of a
59 heritable developmental system that adaptively mitigates stressful environmental conditions
60 (Badyaev 2005, Del Giudice et al. 2018; Ellis & Del Giudice 2019). Such *mitigating* adaptive
61 developmental plasticity is the result of natural selection that favours developmental systems that
62 tend to construct phenotypes that are successful, relative to other variant systems, at surviving and
63 reproducing (Griffiths & Gray 1994). This means that juvenile males can mitigate stress during
64 maturation by refraining from developing costly morphology to maintain fitness and mature and
65 survive as an adult minor, as opposed to risk dying during maturation when investing in costly major
66 morphology (Smallegange et al. 2019). To summarise, in both kinds of adaptive plasticity, the fitness
67 functions of the alternative male phenotypes cross over a condition gradient, but anticipatory
68 adaptive developmental plasticity assumes that the threshold for alternative male phenotype
69 expression at the cross-section of the fitness functions is evolutionarily regulated by how adult males
70 perform, whereas mitigating adaptive developmental plasticity assumes that the threshold is
71 regulated by the dynamics of population density, food competition and individual resource budgets.
72 The fitness functions of both types of developmental plasticity are formalised in the
73 environmental threshold (ET) model (Hazel et al. 1990; 2004). Under the ET model, the alternative
74 expression of phenotypes has been hypothesized to be an environmentally cued threshold trait. It is
75 assumed that threshold traits are based on a continuously distributed, polygenic trait, called the
76 'liability' and a threshold of expression such that individuals that are above this threshold express
77 one phenotype while those below the threshold express the alternative (Roff 1996). Candidate traits

for the liability are, for example, hormone profiles (Roff 1996). The position of the threshold depends on a cue that reliably correlates with the status of the environment, which in many taxa represents condition (Tomkins et al. 2011; Smallegange & Deere 2014). The ET model assumes that, in response to environment-specific selection, alternative phenotypes have evolved different fitness functions, through which selection can affect the distribution of individual liabilities. Because alternative phenotype frequency depends on the distribution of individual liabilities and the cue distribution, both are taken into account in determining how phenotype fitness influences the evolution of liabilities and hence the evolution of a threshold trait. The threshold thus evolves if the fitness functions change in response to changing selection(s), evolutionary impacting alternative phenotype expression. Furthermore, the cue (here: condition) distribution within the ET model informs on population size and structure (Smallegange & Coulson 2013). If the cue (here: condition) distribution, and thus population size and structure, changes, it ecologically impacts what proportion of individuals expresses which alternative phenotype (e.g., a reduction in overall condition reduces the frequency of males that can reach a high enough condition to develop into a fighter). Thus, the ET model gives us the ingredients to create predictions on how changes to the fitness functions and condition distribution of anticipatory or mitigating developmental plasticity fuel eco-evolutionary population change.

We conducted a long-term population experiment to test hypotheses on how anticipatory and mitigating developmental plasticity impact eco-evolutionary population responses to the selective removal of juveniles of different condition in populations of the male polyphenic bulb mite *Rhizoglyphus robini*, using the ET model. Adult fighter males of the bulb mite possess a proportionally thickened third leg pair with dagger-like claws that are used in fights to kill rival males (Radwan et al. 2000). Whereas fighter males metamorphose from good-condition juveniles that have a large resource budget, nutrition-deprived juveniles that grow slow or are of worse condition when metamorphosing into an adult instead express the scrambler phenotype that does not have such leg modifications (Rhebergen et al. 2022). Note that male adult phenotype expression does not

depend on the frequency of each male phenotype in the population (Deere & Smallegange 2014) nor on mite density (Radwan 1995). Further, in response to unfavourable environmental conditions (*e.g.*, low food), *R. robini* expresses a facultative dispersal morph during development, called the deutonymph, which does not feed and is adapted to phoretic dispersal (Díaz et al. 2000). Deutonymph expression occurs mid-development, prior to the final instar stage from which juveniles metamorphose into adults (Díaz et al. 2000), and, thus, prior to when adult male phenotype is determined (which is immediately before metamorphosis [Rhebergen et al. 2022]). Because deutonymph expression carries developmental costs, including reduced size at metamorphosis in both sexes and reduced egg production in females (Deere et al. 2015), our working assumption is that only individuals that are of sufficiently good condition can develop into one if cued by poor environmental conditions. This assumption is supported by the fact that in two of our previous studies (Smallegange & Coulson 2011; Deere et al. 2015), male deutonymphs always matured as a fighter, from which we surmise that males always were in sufficiently good condition to develop costly fighter legs.

In our experiment, we selectively removed individuals of different conditions by removing deutonymphs, or other juveniles. From the ET model, assuming that the male polyphenism is anticipatory, we predict that the ecological response of removing deutonymphs from the population is that it will lower the righthand side of the distribution of individual conditions (because individuals of relatively good condition are removed), and thus population size (compare blue dotted distribution size [before harvesting] with red dashed distribution size [after harvesting for several generations] in Fig. 1c). However, we expect that this will not elicit an evolutionary response because male fitness is assumed to be unaffected by juvenile performance (it is only affected by adult male performance). Thus, we expect that the mean threshold for fighter expression, and thus the proportion of males that are fighters, will track the latter change in the condition distribution because relative, and not absolute condition is important in determining alternative phenotype fitness (Tomkins et al. 2011) (compare the proportions of the differently shaded areas under the

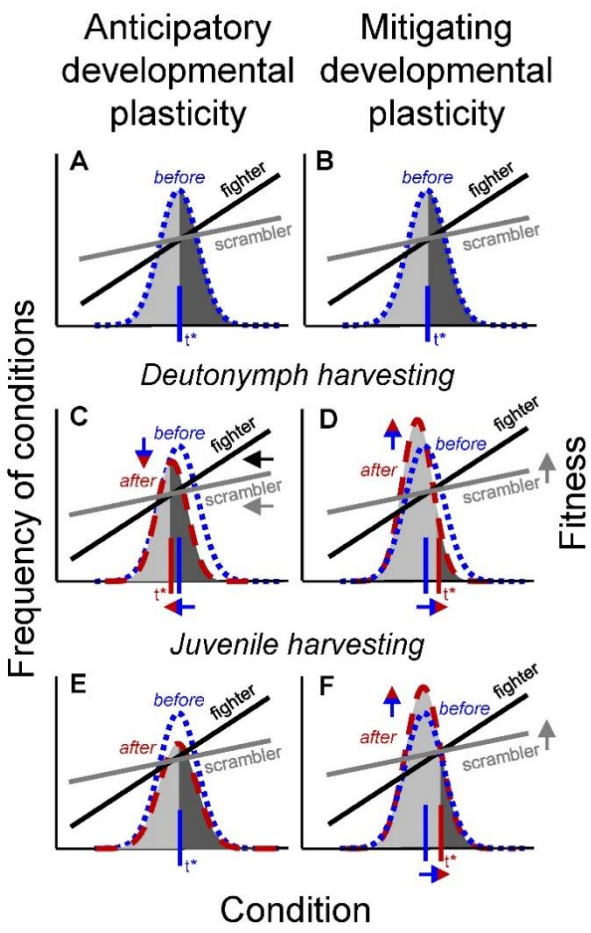


Figure 1. Eco-evolutionary changes due to the selective harvesting of deutonymphs and other juveniles. According to the ET model (Hazel et al. 1990; 2004), fitness functions of fighters (black lines) and scramblers (grey lines) cross over a condition gradient; the area under each condition distribution curve represents population size. The proportion of individuals adopting alternative phenotypes (contrastingly shaded areas under the curves: light grey for scramblers and dark grey for fighters) is determined by the threshold (t^*) condition value at the intersection of the fitness functions (indicated by a vertical line). Blue dotted lines and red dashed lines represent condition distributions before (**a,b**) and after several generations of harvesting (**c-f**), respectively. **(c)** Although the selective harvesting of deutonymphs will reduce the size of the condition distribution (i.e., population size), anticipatory developmental plasticity predicts that the fitness functions, and, thus, the threshold (t^*) for fighter expression, will track the change in the condition distribution and remain in the same, position relative to the condition distribution. In this example, the threshold tracks the mean of the condition distribution. (**e**) Assuming that the harvesting of juveniles reduces population size but does not change mean condition, the threshold (t^*) for fighter expression remains unaffected in case of anticipatory developmental plasticity. (**d,f**) In contrast, the stress mechanism of a developmental system can facilitate the mitigating response to increased deutonymph or juvenile mortality, because males can mature early as a minor to escape the juvenile stage quickly. This will increase scrambler fitness, fuelling the evolution of scrambler expression to a higher threshold (t^*) for fighter expression. Additionally, because scramblers mature earlier in life (Smallegange 2011), live longer than fighters (Radwan & Bogacz 2000) and sire more offspring than fighters (van den Beuken et al. 2019), an increase in scrambler expression can increase population size (Smallegange & Deere 2014), and thus increase the size of the condition distribution (**d,f**).

condition distribution in Fig. 1a [before harvesting] with Fig. 1c [after harvesting for several generations]). Likewise, we predict that the selective removal of juveniles (bar deutonymphs) of random condition has no effect on fighter expression (compare the proportions of the differently shaded areas under the condition distribution in Fig. 1a [before harvesting] with Fig. 1e [after harvesting for several generations]), because fitness functions remain unaltered. The reduction in population size because of the harvesting of juveniles, however, will be reflected in an overall reduced size of the condition distribution (compare blue dotted distribution size [before harvesting] with red dashed distribution size [after harvesting for several generations] in Fig. 1e).

In contrast, according to the ET model and assuming that the male polyphenism is mitigating, the stress mechanism of the developmental system can fuel a mitigating response to increased deutonymph and juvenile mortality because males can mature early as a minor to escape the juvenile stage quickly (Ernande et al. 2004), fuelling the evolution of the threshold for scrambler expression. If scrambler fitness increases relative to that of fighters, the threshold for fighter expression will evolve to decrease, both in response to deutonymph harvesting (compare the proportions of the differently shaded areas under the condition distribution in Fig. 1b [before harvesting] with Fig. 1d [after harvesting for several generations]) and in response to the selective harvesting of other juveniles (compare the proportions of the differently shaded areas under the condition distribution in Fig. 1b [before harvesting] with Fig. 1f [after harvesting for several generations]). Further, because scramblers mature earlier in life (Smallegange 2011), live longer than fighters (Radwan & Bogacz 2000) and sire more offspring than fighters (van den Beuken et al. 2019), an increase in scrambler expression can increase population size (Smallegange & Deere 2014). This ecological response will increase the size of the condition distribution (compare blue dotted distribution size [before harvesting] with red dashed distribution size [after harvesting for several generations] in Fig. 1d and 1f). But note that the removal of good-condition juveniles when removing deutonymphs will result in the right-hand side of the distribution to be at lower condition values (compare blue dotted distribution size [before harvesting] with red dashed distribution size [after harvesting for several generations] in Fig. 1d).

Methods

Study system

The bulb mite has six life stages: egg, larva, protonymph, deutonymph, tritonymph and adult (Fig. 2). The deutonymph stage is a facultative, non-feeding dispersal stage and mites only develop into this stage during unfavourable conditions (i.e. low food quality and quantity) (Díaz et al 2000). When

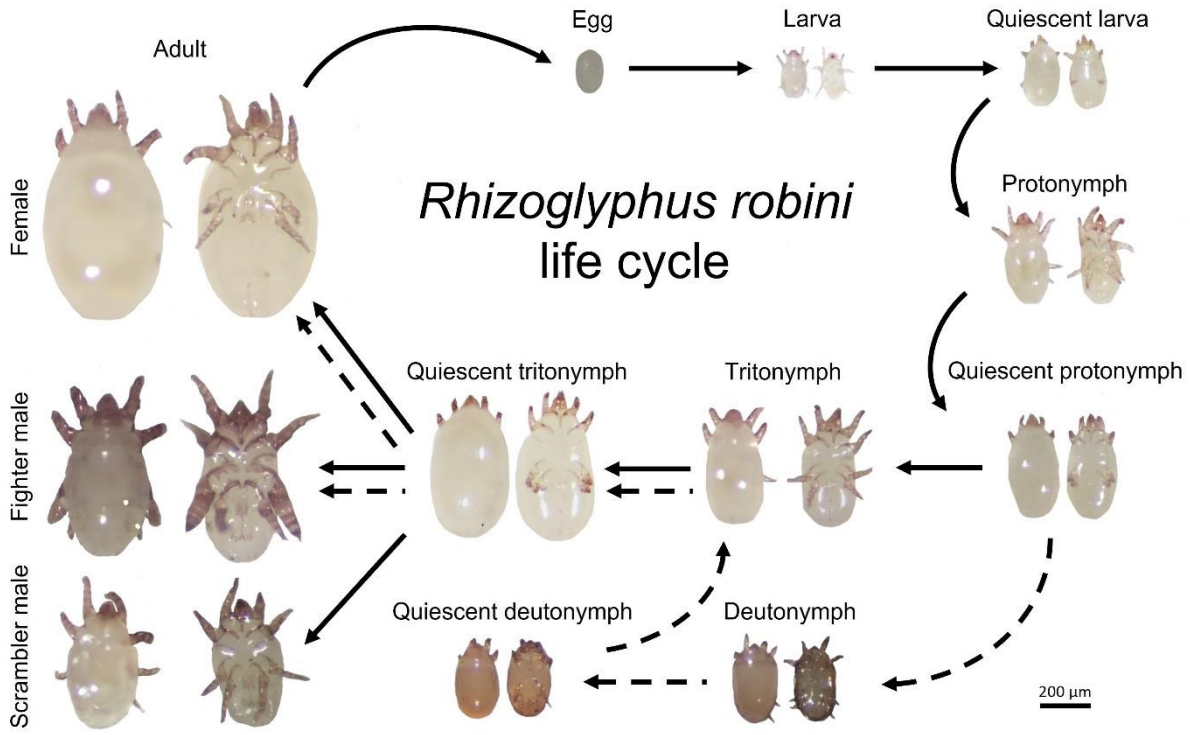


Figure 2. Life cycle of the bulb mite *Rhizoglyphus robini*. The bulb mite has six life stages: egg, larva, protonymph, deutonymph, tritonymph and adult. The deutonymph stage is a facultative, non-feeding dispersal stage and mites only develop into this stage during unfavourable conditions (i.e., low food quality and quantity) (Díaz et al 2000). When growing from one stage to the next, mites moult; this stage is known as the quiescent stage which is immobile and non-feeding. Show are ventral and dorsal images for each stage.

growing from one stage to the next, mites moult; this stage is known as the quiescent stage which is immobile and non-feeding. Source populations were established from mites collected in 2010 from flower bulbs in storage rooms in North Holland. In our source populations, mites rarely develop into a deutonymph and we previously estimated the percentage of males developing into one after removing food and imposing a dry period at 3% (Smallegange & Coulson 2011). Mites were kept on an oats diet and maintained as described in Smallegange (2011). Experimental treatments were established from these source populations (individuals across populations are highly inbred except for scrambler males in stressed environments [Stewart et al. 2019]).

Experimental procedure

The experiment ran between June 2016 and April 2017 (302 days) and comprised five treatments (Fig. 3): weekly harvesting of (i) 100% of all deutonymphs (D100), (ii) 50% of deutonymphs (D50), (iii)

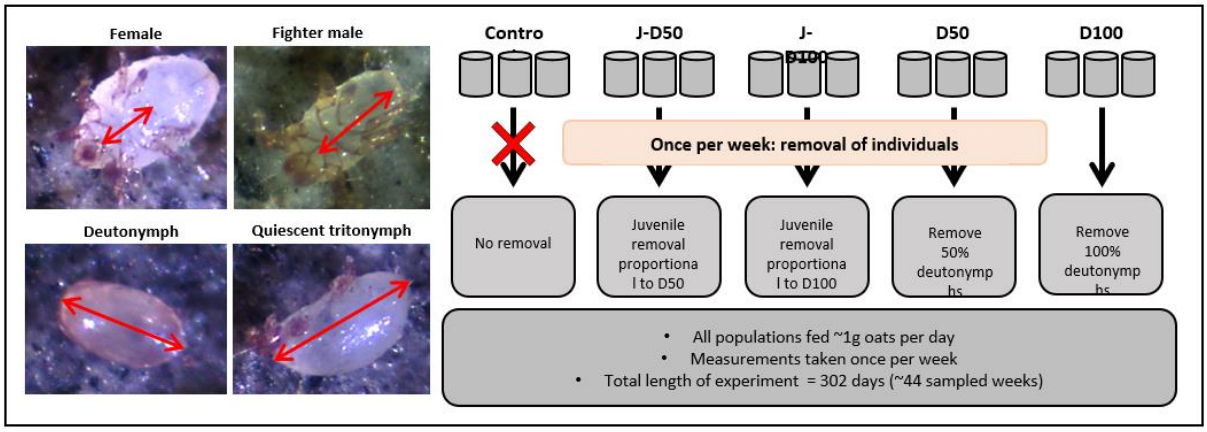


Figure 3. Experimental design. The photos show the length measurements of adult females (top left), adult males (top right), deutonymphs (bottom left) and quiescent individuals (bottom right). The schematic shows the experimental design and harvesting treatments.

other juveniles (excluding eggs and deutonymphs) at the same percentage at which deutonymphs were harvested from all juveniles in D100 (J-D100) to keep the demographic impact of harvesting comparable, (iv) other juveniles (excluding eggs and deutonymphs) at the same percentage at which deutonymphs were harvested from all juveniles in D50 (J-D50), again, to keep the demographic impact of harvesting comparable, and (v) no harvesting (C; general control treatment). Because deutonymph numbers are generally low in our source populations (Smallegange & Coulson 2011), one treatment was to remove all deutonymphs. Two levels of harvesting deutonymphs (D100, D50) and juveniles (J-D100 and J-D50) were chosen to be able to compare harvesting impacts. Because we expect deutonymph numbers to be low, this means that in the other juvenile harvesting treatments, we expect to harvest low numbers as well. We anticipate that these harvesting regimes will still induce population responses. For example, in previous experiments, we also imposed harvesting regimes within which we removed only a few individuals on a regular basis and found these selections to have significant impacts on the threshold for male adult phenotype expression and population size-structure (Smallegange & Deere 2014; Smallegange & Ens 2018). Treatments were replicated three times resulting in fifteen populations. The juvenile harvesting populations were started 8 weeks after the other treatments, but before harvesting commenced (Fig. 4), for logistical reasons. At the point where the juvenile harvesting populations matched the dynamics of the other treatments harvesting started. Populations were kept in 20 mm diameter, flat-bottomed glass tubes

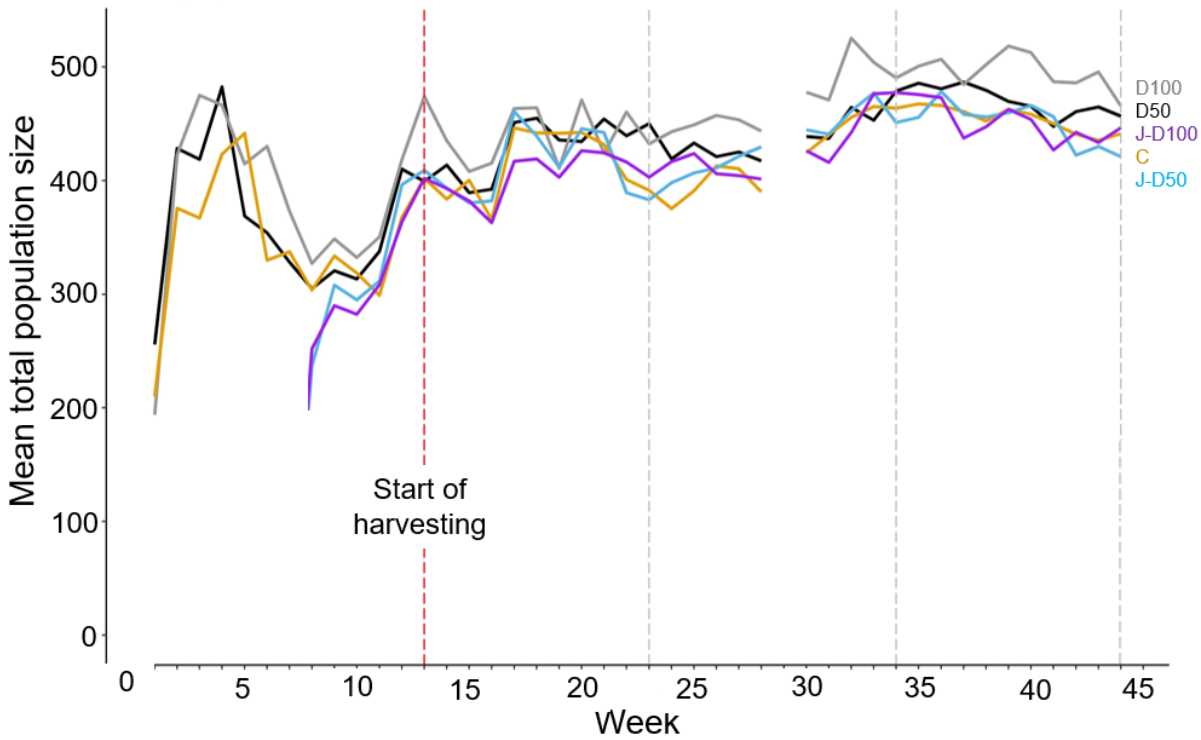


Figure 4. Time series of mean total population size, averaged per harvesting treatment. The treatments were: harvesting of 100% of all deutonymphs (D100: grey line), harvesting of 50% of deutonymphs (D50: black line), harvesting of other juveniles (excluding deutonymphs) at the same percentage at which deutonymphs where harvested from all juveniles in D100 (J-D100: purple line), harvesting of other juveniles (excluding deutonymphs) at the same percentage at which deutonymphs where harvested from all juveniles in D50 (J-D50: indigo line), and no harvesting (C; control treatment: orange line). The harvesting treatments began in week 13 of the experiment. No data were collected in week 29 of the experiment due to illness. Vertical grey lines denote the beginning and end of each time period over which we averaged results (see main text).

with a plaster of Paris and powdered charcoal base, which was kept moist to avoid desiccation of the mites. Tubes were sealed by a circle of very fine mesh (allowing gaseous diffusion), which was held in place by the tubes' standard plastic caps with ventilation holes cut into them. Populations were kept in an unlit climate chamber at 25°C and >70% relative humidity.

Each population was established with 50 randomly selected mites from the source population, which we refer to as founder mites, which we removed after 15 days to reduce founder effects (founder mites can be easily distinguished because they are much bigger than the first generation emerging after 15 days in the experimental population). Each population was fed approximately 1mg of oats per day (the weight was never less than 0.9g and never exceeded 1.1g). After population initialization, on each Thursday, mites of each life stage in all population were counted using a hand counter at 15 X magnification. For three weeks at the start of each time period

257 (day 85-161, day 162-238 and day 239-302: see statistical analyses below), photos were taken of up
258 to 5 (average: 4.05 ± 1.46 SD) individual deutonymphs, fighters, scramblers, and females and their
259 sizes measured as proxies of condition (Rhebergen et al. 2022) to assess any shifts in mean condition
260 across the different life stages in response to experimental conditions. The body length of mites on
261 each photo was measured to the nearest 0.1 µm using ZEN software blue edition (ZEISS microscopy,
262 Carl Zeiss, Germany). We measured body length for adult mites as the ventral distance of the
263 idiosoma (the white bulbous posterior part of the body; from the mouthparts to the furthest part of
264 the genitalia); for deutonymphs as the dorsal anterior-posterior length (without mouthparts); and
265 for quiescent tritonymphs as the lateral body length (without mouthparts) (Fig. 3). Harvesting
266 treatments started 85 days after populations were initialized, which is a sufficiently long time for
267 population numbers to stabilise (which typically happens at 40 days after initialisation [Cameron and
268 Benton 2004; Smallegange and Deere 2014]) (see also Fig. 1). Harvesting was done once a week (on
269 Thursday), after counting and before feeding. The number of individuals harvested in the control
270 populations (J-D100 and J-D50) were calculated based on the proportion of deutonymphs removed
271 from the D100 and D50 populations respectively. The proportion of deutonymphs removed was
272 calculated relative to the combined number of protonymphs and tritonymphs. This proportion value
273 was then applied to the combined number of protonymphs and tritonymphs in the relevant control
274 populations (proportion value for D100 (D50) was applied to J-D100 (J-D50)). The proportion value
275 applied to the populations calculated the total number of individuals to remove from the J-D100 and
276 J-D50 populations. Only protonymphs and tritonymphs were removed from the control populations
277 and this was done randomly. The total protonymphs and deutonymphs removed for each population
278 for each week can be found in data file in the online appendix (Smallegange and Deere 2023). The
279 harvesting treatments were applied for a total of 217 days, which in a similar experiment was
280 sufficient to observe an evolutionary shift in fighter expression (Smallegange & Deere 2014).
281 However, even if this period of time is too short to observe an evolutionary response to harvesting,
282 we can still distinguish between our anticipatory and mitigating hypotheses. Specifically, under

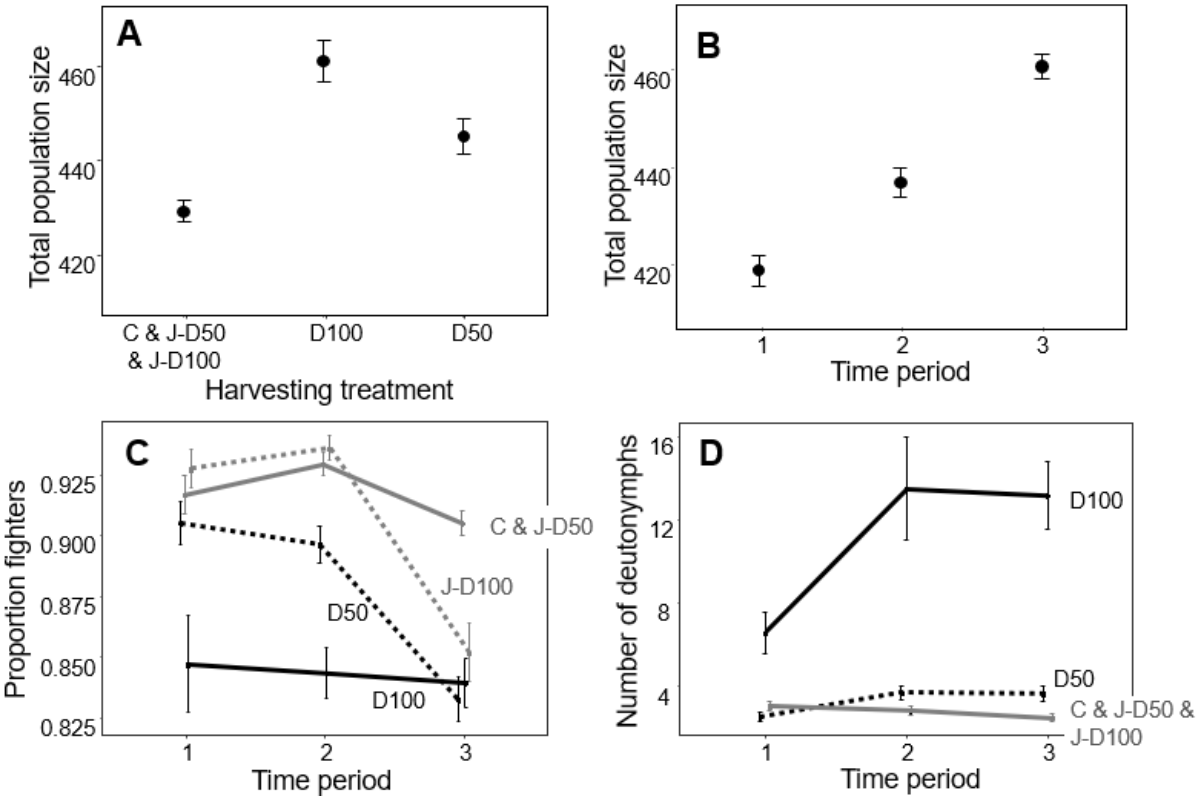
283 juvenile harvesting (J-100 and J-D50), fighter expression is predicted to remain unaltered if it is
284 anticipatory (Fig. 4e). However, fighter expression is predicted to decrease if it is mitigating (Fig. 4f)
285 because juvenile males can respond quickly (within a generation) to increased juvenile mortality by
286 expediating ontogeny and mature as a scrambler. This plastic (ecological) response, in turn, will
287 further fuel the evolution towards developmental systems that produce scramblers in response to
288 the juvenile harvesting selection pressure. What is important to note is that the ET model states that
289 any change in the threshold for alternative male phenotype expression will affect the proportion of
290 individuals developing either phenotype because it is expected to track the intersection of the
291 alternative phenotype fitness functions. Therefore, we can deduce evolutionary shifts in the
292 threshold from evolutionary changes in fighter expression (the proportion of adult males that are
293 fighters).
294
295 *Life-history assays*
296 Following the end of the long-term population experiment we conducted a common garden life
297 history assay to assess if any differences in body size (which we assume to approximate condition)
298 and fighter expression between treatments were plastic or genetic. Logistical constraints prevented
299 us from conducting the time-consuming and labour-intensive assays to measure the threshold for
300 alternative male phenotype expression itself. For each assay we removed ten adult females from
301 each population, individually isolated them and gave them ad lib access to oats and allowed them to
302 lay eggs. Three of the ten females (isolating more individuals was logistically not possible) were then
303 randomly selected and their offspring individually isolated, given ad lib access to oats, and followed
304 until they reached maturity. Deutonymphs, quiescent tritonymphs and adults (2-5 days after
305 maturation) were size-measured as above and their sex and morph scored (we measured a total of
306 420 individuals). The effects of maternal nutritional conditions on size, age and adult male
307 phenotype are negligible in this species (the effect size of offspring environment is 15 times larger
308 than that of maternal environment: Smallegange 2011a), therefore, rearing mites in a common

309 garden environment condition for one generation is sufficient to eliminate maternal effects. Females
310 and their offspring were kept in 10 mm diameter tubes with a plaster of Paris and powdered
311 charcoal base, which were kept in an unlit climate chamber at 25°C and >70% relative humidity.
312
313 *Statistical analyses*
314 To analyse the results from the population experiment, we only used data from day 85 onwards
315 (when harvesting commenced) and excluded two population tubes that had fallen over during the
316 population experiment (one tube in treatment D100 and one in treatment J-D50). We then divided
317 the experimental period into three periods, day 85-161, day 162-238 and day 239-302 to assess
318 long-term (instead of transient) temporal changes in the response variables within each treatment
319 group. To analyse the results of the population experiment, we used a generalised linear mixed
320 model (GLMM) with Gaussian errors to analyse the effect of the fixed factors harvesting treatment
321 (C, D100, D50, J-D100, J-D50) and time period (period 1, 2, and 3) and their interaction, including
322 'population tube' as a random effect (to account for the repeated measures within each
323 experimental population) on: fighter expression (the number of fighters with the number of adult
324 males set as an offset so that the model prediction will be proportion of fighter males), and the
325 mean size of deutonymphs, adult fighters, scramblers and females. The model assumptions of
326 Gaussian errors and homoscedacity were confirmed by inspecting the probability plots and error
327 structures. We used a GLMM with Poisson errors to analyse the effects of the fixed factors
328 harvesting treatment and time period, their interaction, with 'population tube' as a random effect,
329 on the number of deutonymphs and on total population size. In the online appendix (Smallegange
330 and Deere 2023) we present the analysis of treatment effects on the number of juveniles and female
331 and male adults.
332 To analyse the results of the life history assay conducted at the end of the population
333 experiment, we used a GLMM with Gaussian errors to analyse the effect of the fixed factor
334 harvesting treatment (C, D100, D50, C-D100, C-D50), including 'population tube' and 'maternal

335 identity' as random effects on the mean size of adult fighters, scramblers and females. The model
336 assumptions of Gaussian errors and homoscedacity were again confirmed by inspecting the
337 probability plots and error structures. We used a GLMM with binomial errors to analyse the effect of
338 the harvesting treatment on fighter expression ('0' if a male developed into a scrambler, and '1' if in
339 a fighter), including 'population tube' and 'maternal identity' as random effects.
340 In each GLMM, the significance of the treatment effects was tested using a model
341 simplification procedure, whereby the full model was fitted after the least significant term had been
342 removed (never deleting random terms from the model), if the deletion caused an insignificant
343 increase in deviance as assessed by a maximum likelihood ratio test (LRT). Pairwise comparisons
344 among the treatment levels were conducted by creating a reduced model within which two levels
345 were combined. If the reduced model caused an insignificant increase in deviance as assessed by a
346 maximum likelihood ratio test (α = 0.05), then the two levels were considered to be not significantly
347 different. All analyses were conducted in R and for all GLMMs we used the *lme4* package (www-r-
348 project.org).
349
350 **Results**
351
352 *Population size, fighter expression and number of deutonymphs*
353 Mean total population size slightly increased over time since we started harvesting (Fig. 4). Indeed,
354 mean population size significantly differed between time periods (χ^2_2 = 262.07, p<0.001) (non-
355 significant interaction: χ^2_8 = 7.30, p=0.063) and was also significantly affected by harvesting (χ^2_4 =
356 15.58, p=0.004). Population size was highest when 100% of deutonymphs were harvested (D100),
357 lower when 50% of deutonymphs were harvested (D50), and lowest in all the other treatments (C, J-
358 D50 and J-D100) (treatments C and J-D50 did not differ significantly (χ^2_1 = 0.35, p=0.553), and neither
359 did C and J-D50 differ significantly from J-D100 (χ^2_1 = 0.47, p=0.494)) (Fig. 5A). Irrespective of

360 harvesting treatment, total population size significantly increased with increasing time period (Fig.

361 5B).



362 **Figure 5. Population size and structure of the long-term population experiment.** Mean total population size
363 differed between different harvesting treatments **(a)** and between the different time periods **(b)**. Fighter
364 expression varied over time in most but not all harvesting treatments **(c)**. The number of deutonymphs also
365 varied over time in some but not all harvesting treatments **(d)**. Errors in all panels are standard errors.
366 Harvesting treatments were: harvesting of 100% of all deutonymphs (D100: solid black lines), harvesting of
367 50% of deutonymphs (D50: dashed black lines), harvesting of other juveniles (excluding deutonymphs) at the
368 same percentage at which deutonymphs where harvested from all juveniles in D100 (J-D100: grey dashed line
369 (c) and solid grey line (d)), harvesting of other juveniles (excluding deutonymphs) at the same percentage at
370 which deutonymphs where harvested from all juveniles in D50 (J-D50: solid grey lines), and no harvesting (C;
371 control treatment: solid grey lines). Treatment levels that did not significantly differ from each other are
372 grouped (see main text). Note that y-axes do not start at zero.

373 The harvesting treatment significantly affected the proportion of fighters but differently at

374 different time periods (significant interaction harvesting × time period: Σ_8^2 = 29.92, p<0.001). Within

375 the interaction, the harvesting treatments C and J-D50 did not significantly differ in their effect on

376 proportion of fighters in the different time periods (χ_3^2 = 4.22, p=0.239) and were combined into one

377 level. The next two similar responses to the harvesting treatments J-D100 and D50 did, however,

378 differ significantly (χ_3^2 = 11.80, p=0.008) (Fig. 5C). In summary, the proportion of fighters was always

379 relatively the lowest when 100% of deutonymphs were harvested (D100 treatment) (Fig. 5C), but
380 when other juveniles were harvested at the same percentage as in D100, (J-D100), and when
381 harvesting 50% of deutonymphs (D50), the proportion of fighters was relatively high in the first time
382 periods, but lower in the last time period (Fig. 5C). In contrast, under the combined harvesting
383 treatments of C and J-D50, the proportion of fighters was always high over the whole course of the
384 experiment (Fig. 5C).

385 The harvesting treatment also significantly affected the number of deutonymphs, but, again,
386 differently at different time periods (significant interaction harvesting × time period: χ^2_8 = 49.70,
387 p<0.001). Within the interaction, the harvesting treatment levels J-D100 and C did not significantly
388 differ (χ^2_3 = 0.40, p=0.940) and were combined into one level. Likewise, the latter combined level did
389 not significantly differ from the J-D50 harvesting treatment (χ^2_3 = 3.08, p=0.380) and all three control
390 levels were combined into one level. These three levels, combined, significantly differed from the
391 D50 harvesting level (χ^2_3 = 12.42, p=0.006) and from the D100 harvesting level (χ^2_3 = 67.71, p<0.001).
392 We therefore find that, counterintuitively, the number of deutonymphs was higher in the last time
393 period than in the first one when all deutonymphs were harvested (D100), and, to a lesser extent,
394 when 50% of deutonymphs were harvested (D50) (Fig. 5D). In contrast, in the other treatments
395 combined, the number of deutonymphs was slightly lower in the last time period than in the first
396 (Fig. 5D). Furthermore, at any given time period, the number of deutonymphs was always the
397 highest in the treatment where weekly harvesting removed all deutonymphs (D100) (Fig. 5D). In the
398 online appendix (Smallegange and Deere 2023), we present interaction plots for the three response
399 variables.

400

401 *Deutonymph, fighter, scrambler and adult female mean size*

402 Mean deutonymph size was not significantly affected by harvesting (χ^2_4 = 4.81, p=0.307) but
403 decreased with each consecutive time period (significant effect of time period: χ^2_2 = 106.31, p<0.001)

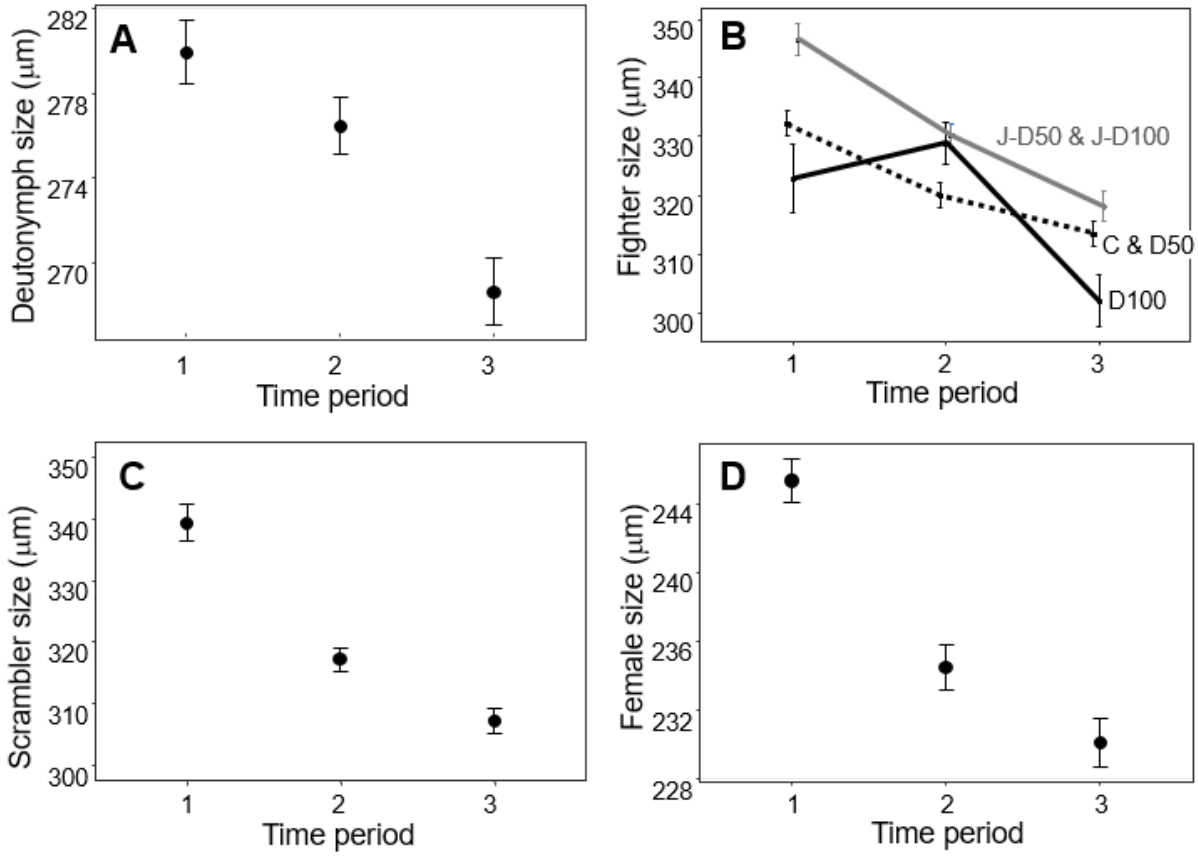


Figure 6. Mean body sizes observed in the long-term population experiment. Mean deutonymph size (μm) **(a)**, mean fighter size (μm) **(b)**, mean scrambler size (μm) **(c)** and mean female size (μm) **(d)** all significantly decreased over the course of the experiment, but for fighters, this decrease differed between harvesting treatments (d). Errors in all panels are standard errors. Harvesting treatments were: harvesting of 100% of all deutonymphs (D100: solid black line), harvesting of 50% of deutonymphs (D50: dashed black line), harvesting of other juveniles (excluding deutonymphs) at the same percentage at which deutonymphs where harvested from all juveniles in D100 (J-D100: grey solid line), harvesting of other juveniles (excluding deutonymphs) at the same percentage at which deutonymphs where harvested from all juveniles in D50 (J-D50: grey solid line), and no harvesting (C; control treatment: dashed black line). Treatment levels that did not significantly differ from each other are grouped (see main text). Note that y-axes do not start at zero.

(Fig. 6A) (non-significant interaction: χ^2_8 = 7.22, p=0.513). Mean fighter size showed a similar response but size differed significantly between the different harvesting treatments (significant interaction harvesting × time period: Σ^2_8 = 19.44, p=0.013) (Fig. 6B). Within the interaction, fighter size in the harvesting treatment levels J-D50 and J-D100 did not significantly differ (χ^2_3 = 2.33, p=0.507) and were combined into one level (Fig. 6B). Similarly, fighter size in the harvesting treatment levels C and D50 did not significantly differ (χ^2_3 = 1.83, p=0.609) and were combined into one level (Fig. 6B). The overall result was that mean fighter size in the combined levels J-D50 and J-

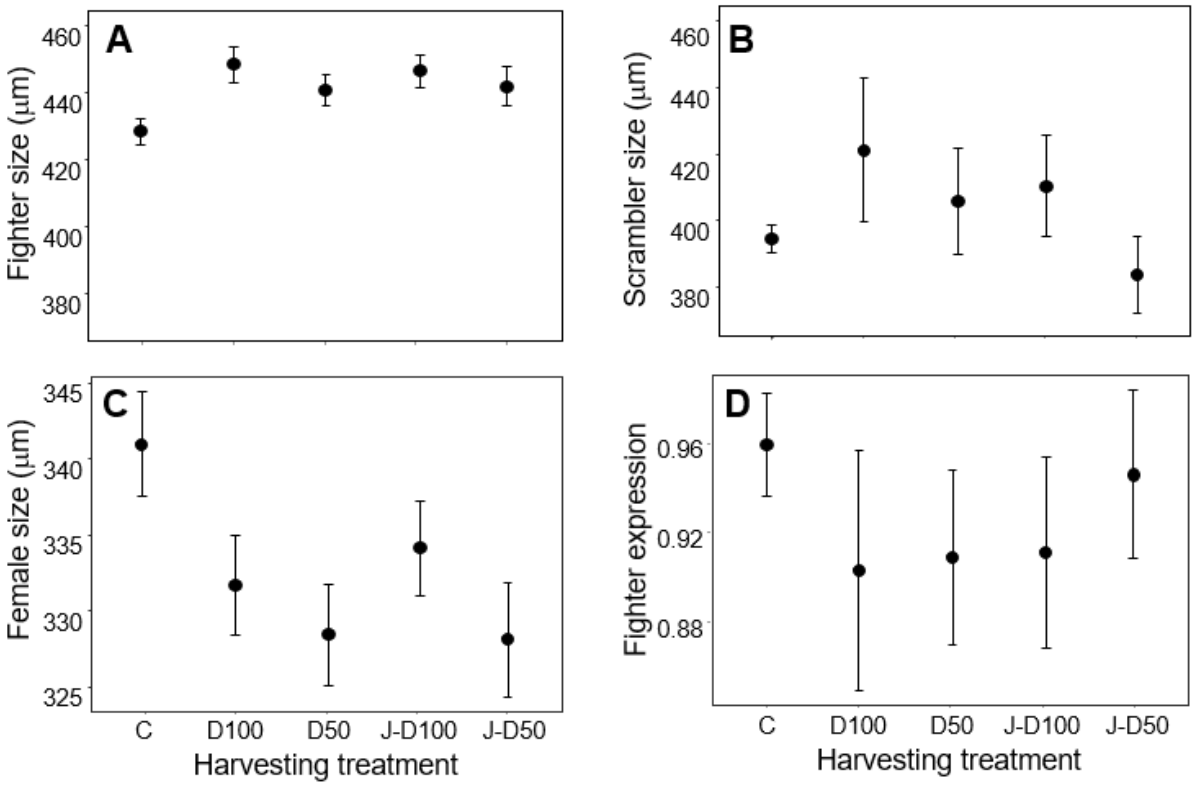


Figure 7. Life history assay results. Mean scrambler size (μm) **(a)** and mean fighter expression **(b)** for each harvesting treatment. Errors in all panels are standard errors. Harvesting treatments were: harvesting of 100% of all deutonymphs (D100), harvesting of 50% of deutonymphs (D50), harvesting of other juveniles (excluding deutonymphs) at the same percentage at which deutonymphs where harvested from all juveniles in D100 (J-D100), harvesting of other juveniles (excluding deutonymphs) at the same percentage at which deutonymphs where harvested from all juveniles in D50 (J-D50), and no harvesting (C; control treatment). Note that y-axes do not start at zero and differ between panels.

D100 and in the combined levels C and D50 was lower in the last than in the first time period, whereas mean fighter size in the D100 treatment did not decrease until the last time period (Fig. 6B). Mean scrambler size was not significantly affected by harvesting (χ^2_4 = 1.17, p=0.883) but was significantly lower in each consecutive time period (significant effect of time period: χ^2_2 = 96.44, p<0.001) (Fig. 6C) (non-significant interaction: χ^2_8 = 9.48, p=0.303). Finally, mean adult female size was also not significantly affected by harvesting (χ^2_4 = 0.62, p=0.961) but significantly decreased with each consecutive time period (significant effect of time period: χ^2_2 = 67.65, p<0.001) (Fig. 6D) (non-significant interaction: χ^2_8 = 14.55, p=0.068). In the online appendix (Smallegange and Deere 2023), we present interaction plots for the four response variables.

437 *Life history assay*

438 Neither fighter size (Σ_4^2 = 6.58, p=0.160, mean size: 439.76 μm ± 2.39 SE, n = 190) (Fig. 7A), scrambler
439 size (Σ_4^2 = 2.77, p=0.597, mean size: 401.07 μm ± 7.33 SE, n = 14) (Fig. 7B) or female adult size (Σ_4^2 =
440 3.75, p=0.440, mean size: 334.66 μm ± 1.65 SE, n = 206) (Fig. 7C) were affected by the harvesting
441 treatments in the common garden life history assay. Fighter expression was also not significantly
442 affected by harvesting treatment (Σ_4^2 = 0.51, p=0.973) (Fig. 7D); however, only 14 scramblers
443 emerged in the life history assay (as opposed to 190 fighters), prohibiting any statistical inference.
444

445 **Discussion**

446 We tested two hypotheses on how developmental plasticity impacts the eco-evolutionary response
447 of male polyphenic bulb mite populations to the selective removal of individuals of different
448 developmental stages. If alternative male phenotype expression is taken to be anticipatory
449 (anticipating future mating success), we predicted that the selective harvesting of deutonymphs and
450 other juveniles would not impact fighter expression. In contrast, if alternative male phenotype
451 expression is taken to be mitigating, we predicted that the selective harvesting of deutonymphs and
452 other juveniles would decrease fighter expression both plastically, as male juveniles can expediate
453 development and escape the juvenile stage quicker by maturing as a scrambler, and evolutionarily,
454 as the selective removal of juveniles fuels the evolution of developmental systems that produce
455 scramblers. In line with the mitigating hypothesis, we found that fighter expression was overall
456 lowest when 100% of all deutonymphs were harvested (D100), and, at the end of the experiments,
457 had reached similarly low levels in the treatments where 50% of deutonymphs were harvested (D50)
458 and where the highest number of other juveniles were harvested (J-D100). This 'delayed' response
459 could be due to that fact that our proportional harvesting treatments became more severe as
460 population size increased over the course of the experiment. In contrast, fighter expression
461 remained high throughout the experiment in the control treatment and in the treatment where the
462 lowest number of juveniles were harvested (J-D50), perhaps because, there, the harvesting impact

was the lowest. Our life history assay at the end of the population experiment did not have sufficient statistical power to tell if these shifts in fighter expression were (in part) evolutionary. However, it is striking that the harvesting treatments where we observed the lowest levels of fighter expression in the population experiment are the same as where we observed the lowest fighter expression levels in the life history assay. But even if this pattern was coincidental and not indicative of an evolutionary change in fighter expression, our findings still point to a role for mitigating developmental plasticity. That is, we expected no shift in fighter expression at all in response to the harvesting of juveniles (bar deutonymphs) under anticipatory developmental plasticity (Fig. 1e), but a reduction in fighter expression under mitigating developmental plasticity (Fig. 1f) because individuals mature earlier as a scrambler to escape the risky juvenile stage. The latter reduction is indeed what we observed towards the end of the experiment in the treatment where we harvested the highest number of juveniles other than deutonymphs (J-D100). Our results therefore suggest that nutrition-deprived male juveniles do not 'make the best of a bad job' by anticipating a non-fighting mating tactic (Dawkins 1980; Eberhard 1982), but instead develop into that male adult phenotype because they can adaptively mitigate their early-life stress (Rhebergen 2022). Such adaptive early-life stress responses that have negative effects in adulthood are common in (warm-blooded) mammals and birds (Lindström 1999; Fisher et al. 2006; Wells 2011; Vickers 2014), likely because their growth during development is physiologically constrained. However, if we account for such pre-adult viability selection in coldblooded species that typically show flexible growth, it would allow us to better characterise natural selection on trait development like male polyphenisms in these species, how it can affect the response to other selections in adulthood (e.g., sexual selection: Mojica and Kelly 2010; Lürig & Matthews 2021; Rhebergen 2022), and how such trait dynamics influence, and are influenced by, population dynamics (Smallegange 2022).

One unexpected finding in our experiment was that the number of deutonymphs was highest when we harvested all of them, each week. Further, despite being harvested, deutonymph number increased as the experiment progressed. We can only speculate why this happened.

Perhaps this overcompensatory response was because the per capita food availability increased as we removed individuals (Verhulst 1838, Schaefer 1954, Hilborn and Walters 1992), although we still only maximally removed a small percentage of the total population in the deutonymph harvesting treatments. It could also be simply a numerical response because mean total population size increased over the course of the experiment and thus there were more individuals that could develop into a deutonymph. Alternatively, initiation of the deutonymph stage in this species is due to poorer resource availability and so our findings are unlikely due to an increase in per capita food availability. Finally, the higher number of deutonymphs we found could also reflect eco-evolutionary dynamics in which another selection pressure, for example imposed by strong-density dependence (population size was highest in the 100% deutonymph harvesting treatment), opposed the effects of direct harvesting (Edeline & Loeuille 2021). Or, perhaps, because twice as many females emerge from deutonymphs than males (fighters) (Deere et al. 2015; Stewart & Smallegange in prep), removing deutonymphs reduces females and egg output, reducing density-dependence. Either way, failure to account for either of these eco-evolutionary processes might fundamentally hamper our ability to understand the expression of dispersal phenotypes. Finally, in our previous studies (Smallegange & Coulson 2011; Deere et al. 2015), male deutonymphs always matured as a fighter, but here, increases in deutonymph numbers did not coincide with increases in fighter frequency. Perhaps this was because twice as many females emerge from deutonymphs than males (fighters) (Deere et al. 2015; Stewart & Smallegange in prep) so that our statistical analyses were unable to pick up significant differences in the few more fighters that emerged. It does highlight, however, that we still have some way to go to unravel the intricate links between deutonymph expression, alternative male phenotype expression and sex ratio and how they together drive population dynamics.

Because a change in the distribution of a trait will almost always also change the size of the distribution of that trait, it follows that trait change is accompanied by a change in population size. If a trait is heritable, this constitutes eco-evolutionary change at the population level (Smallegange &

515 Coulson 2013). This is especially so in the case of alternative phenotypes where we expect a shift in
516 phenotype expression to be accompanied by a change in population size because the different
517 phenotypes often have different demographic rates. For example, in the case of bulb mite males,
518 scramblers mature earlier in life (Smallegange 2011), live longer than fighters (Radwan & Bogacz
519 2000) and sire more offspring than fighters (van den Beuken et al. 2019) so that an increase (or
520 decrease) in scrambler (or fighter) expression will increase population size. Indeed, we found the
521 highest population size in the harvesting treatment with the lowest level of fighter expression (D100:
522 100% deutonymph harvesting). We suspect that the increase in population size that we observed
523 over the course of the experiment is associated with the observed decrease in mean body size over
524 time in response to the strong, density-dependent food conditions, because smaller organisms
525 typically reproduce faster and can reach higher equilibrium population sizes than larger ones (e.g.,
526 Huryn & Benke 2007). Indeed, Gilbert et al. (2022) recently showed in an experiment with the protist
527 *Tetrahymena pyriformis* that mean body size decreased in response to increased density-
528 dependence and that this rapid change in mean body size had a larger effect on population density
529 than the reverse. Reductions in mean body size have been observed across a range of taxa in
530 response to adverse environmental change (Gardner et al. 2011; Sheridan & Bickford 2011). Often,
531 these reductions are associated with increased mortality rates (e.g., in red knots *Calidris canutus*
532 [van Gils et al., 2016]). What is more, when populations not only suffer from directional
533 environmental change but also from selective harvesting, the removal of good condition individuals
534 (of large size) can lead to population extinction (Knell & Martínez-Ruiz 2017). Thus, unravelling the
535 intertwined ecological and evolutionary dynamics of population size, body size, condition and
536 condition-dependent (alternative) phenotypes is integral to understanding eco-evolutionary
537 population responses to change (Edeline & Loeuille 2021).

538 **Data availability statement**

539 The raw data, the R scripts that we used to analyse the data, and the additional analyses on

540 population structure can be found on Figshare (Deere & Smallegange 2023).

541

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