OIKOS

Research

Population consequences of individual heterogeneity in life histories: overcompensation in response to harvesting of alternative reproductive tactics

Isabel M. Smallegange, Rianne E. Fernandes and Jasper C. Croll

I. M. Smallegange (http://orcid.org/0000-0001-6218-7358) (i.smallegange@uva.nl), R. E. Fernandes and J. C. Croll, Inst. for Biodiversity and Ecosystem Dynamics (IBED), Univ. of Amsterdam, PO Box 94240, NL-1090 GE Amsterdam, the Netherlands.

Oikos
127: 738–749, 2018
doi: 10.1111/oik.04130

Subject Editor: Yngvild Vindenes
Editor-in-Chief: Dries Bonte
Accepted 16 April 2017

Alternative reproductive tactics (ARTs) are examples of individual heterogeneity in which males adopt one of typically two alternative strategies to mate with females: males are either large, armed fighters or small, benign sneakers. ART expression is often conditionally determined, and variation in the expression of conditional ARTs due to genetic and/or environmental influences can greatly affect population composition and trajectory. For example, ecological feedback mechanisms resulting from strong density-dependent competition over food have been suggested to explain the observation that the harvesting of scramblers (= sneakers) in closed populations of the bulb mite *Rhizoglyphus robini* did not result in an increase (expected from quantitative genetics theory) but decrease in fighter expression. Here, we exposed closed bulb mite populations to selective fighter or scrambler harvesting for 5–6 generations under abundant food (to halt ecological feedbacks through density-dependence) to confirm predictions from quantitative genetics theory. However, we found no evolutionary shift in ART expression; rather, we observed an overcompensatory ecological response, whereby the number of fighters increased when we harvested them. Treatment effects on scrambler numbers could not be tested as there were too few in the experimental populations. Further experiments revealed that starved fighters preferentially killed immature males and immature fighters; possibly to reduce male–male competition as e.g. immature fighters have not yet developed their lethal weaponry. If this is so, then harvesting adult fighters reduced the killing pressure on immature males in our experiment, which resulted in an overcompensatory number of immature fighters that matured as adults. Our results highlight the complexity of how individual heterogeneity in ARTs affects the ecological and evolutionary processes that determine population fluctuations.

Introduction

Environmental change can elicit concurrent change in ecological quantities, such as population density and structure, as well as in evolutionary quantities such as shifts in the distributions of genetically based phenotypic characters (Schoener 2011).

Phenotypic change, in turn, can influence population size and structure, creating so-called eco-evolutionary feedbacks (Smallegange and Coulson 2013). A change in population structure implies a change in the frequency distribution of individuals that can be characterised according to different properties (e.g. size, developmental stage and reproductive tactic). If individuals with different characteristics also follow different life history trajectories and respond differently to environmental change, such individual heterogeneity can create complex interactions between the ecological and evolutionary processes that determine population fluctuations (Cameron et al. 2013, Smallegange and Deere 2014, Vindenes and Langangen 2015). Because biologists face the challenge of accurately predicting how populations with different structures respond to ever-greater environmental change, it is essential to understand how individual heterogeneity affects the eco-evolutionary interactions that determine population fluctuations.

Prominent examples of individual heterogeneity within populations are male alternative reproductive tactics (ARTs). Male ARTs occur in a wide range of taxa, including birds, fish, insects, mites and isopods, and typically involve adult males following one of two, permanent-for-life strategies: a fighter strategy, in which males have morphological structures that act as weapons in male–male competition over access to females; or a sneaker strategy, in which males are smaller, do not have weapons, and sneak or engage in scramble competition over access to females (Gross 1991, Shuster and Wade 1991, Kotiaho et al. 2003, Oliveira et al. 2008, Radwan 2009). In most species, male morph expression critically depends upon the environmental conditions experienced during development (food, population density and population structure) (Roff 1996, Tomkins and Hazel 2007, Smallegange 2011, Smallegange and Deere 2014), in which case male morph expression is classified as a conditional strategy (Tomkins and Hazel 2007). Because it is unlikely that individuals experience exactly the same environmental conditions during ontogeny because they genetically differ in their sensitivity to environmental conditions or because they experience different conditions, individuals will vary in their life history trajectories. This life history variation in turn influences male ART expression within populations, and it is this rationale that forms the basis of the environmental threshold (ET) model. The ET model is currently the favoured explanation for the evolution of conditional strategies (Hazel et al. 1990, 2004, Tomkins and Hazel 2007). The ET model assumes that a continuously distributed, polygenic trait called the 'liability' underlies a threshold of expression, so that individuals that during a critical point in ontogeny have a liability value above this threshold express one phenotype, whilst those with a liability value below the threshold express the alternative. The liability value relates to a cue that reliably correlates with environmental conditions, which in many taxa is body size (Roff 1996, Kotiaho et al. 2003, Smallegange 2011). The ET model assumes that alternative phenotypes have evolved different fitness functions through which selection can affect the evolution of a threshold trait, such as ART expression. The ET model predicts that selection against one tactic results in a reduction in the expression of that tactic in the population (Tomkins and Hazel 2007), which has been successfully tested in a male-dimorphic mite *Rhizoglyphus echinopus* using a discrete-generation method (Tomkins et al. 2011) that prohibits population feedback in experimental populations (because a sample of individuals from one generation is used to start the next; Santos et al. 1997, Kolss et al. 2009, Radwan 2003). In male morph selection experiments with *Rhizoglyphus robini*, we used both the discrete-generation and the overlapping-generation methods (Smallegange and Coulson 2011, Smallegange and Deere 2014). In contrast to the discrete-generation method, experimental populations in the overlapping generation method are left intact (except for any effects through experimental treatments) so that there is continuous reproduction (and hence overlapping generations) and population feedback through e.g. density-dependence. Our results from the discrete-generation experiment confirmed predictions from the ET model (Smallegange and Coulson 2011), but in the overlapping-generation experiment, we found that regardless of which male morph was targeted, the direction of evolution of male morph expression in response to selection was always towards sneaker mites, which are called scramblers (Smallegange and Deere 2014). The latter result contradicts the prediction from the ET model that selection against scramblers would result in a decrease (and not an increase) in scrambler expression. Unravelling the mechanism that drives this mismatch between empirical results on ART expression and classic evolutionary theory would be an important step in understanding how individual heterogeneity and eco-evolutionary feedbacks determine population fluctuations.

Here, we aimed to solve the mismatch between predictions from classic evolutionary theory on ART expression and experimental observations from selection experiments in closed populations to increase our understanding of how eco-evolutionary feedbacks that are related to ART expression determine population fluctuations. In closed populations, scrambler harvesting resulted in a decrease in fighter, not scrambler, expression in *R. robini* (Smallegange and Deere 2014). Because individuals in these experimental populations experienced high density-dependent competition over food, this result is likely driven by ecological feedback mechanisms resulting from the high density-dependence. Smallegange and Deere (2014), for example, hypothesized that the selective scrambler harvesting selected against fighter expression because it deprived fighters of cannibalism opportunities in the food-limited experimental populations (in the Discussion we also present alternative explanations). Based on these results, we would expect to find a positive effect on fighter expression when harvesting scramblers from experimental populations if density-dependent competition over food is minimised and, thereby, ecological feedback mechanisms halted. In this study, we tested this hypothesis by repeating the

harvesting procedures conducted by Smallegange and Deere (2014), but provided the experimental *R. robini* populations with ad libitum access, instead of limited access, to food (yeast). In this way, we aimed to maximally reduce density-dependent competition over food. In the absence of any ecological feedbacks resulting from density-dependent competition over food, based on the ET model, we hypothesise that selecting against fighters (or scramblers) by applying proportional harvesting regimes to fighters (or scramblers) would result in a decrease in fighter (or scrambler) expression (Smallegange and Deere 2014, Appendix). Our population experiment was conducted over six generations, which was sufficiently long to elicit an evolutionary response to selection on male morph expression in our *R. robini* populations, both in a discrete-generation (Smallegange and Coulson 2011) and in an overlapping-generation experiment (Smallegange and Deere 2014). However, note that Radwan (2003) found a significant response over six generations in only one out of the two discrete-generation experiments on male morph expression in *R. robini* that he conducted. At the end of the population experiment, we performed a common environment life history assay to assess whether the change in male morph expression recorded over the course of the experiment was plastic or genetic. Fighters are known to kill large conspecific juveniles and small conspecific adults, for example to reduce male–male competition (Radwan et al. 2000) or for nutrient uptake (Łukasik 2010), which could drive ecological feedbacks in this ART system. We therefore also explored the killing behaviour of fighters by conducting two survival experiments to assess if the survival probabilities of individual final instars (tritonymphs), adult females, scramblers and fighters were reduced in the presence of a starved fighter.

Methods

Source population and *Rhizoglyphus robini* life cycle

Bulb mites (Acaridae) live in the soil and feed on bulbs and tubers, and are pests of many crops and ornamentals (Díaz et al. 2000). They are small (100–1000 μm) and live for up to a few months. From egg to adult, they go through a larval and two to three nymph stages, which takes between 11–40 days depending on food quality (under constant temperature of 25°C) (Smallegange 2011). Our mites were collected from flower bulb storage rooms in the Netherlands in December 2010 and maintained on yeast, as described in Smallegange (2011). The life cycle of the bulb mite consists of six stages: egg, larva, protonymph, deutonymph, tritonymph and adult. The deutonymph is a facultative dispersal stage that escapes unfavourable environmental conditions, and its development is induced by low food quality and quantity (Díaz et al. 2000). None were observed in this study. For the population experiment, all of the juvenile stages (larva, protonymph and tritonymph) were placed into a single category and scored as juveniles. Only adult males (not juveniles) display the different male morphologies (fighter or scrambler). Whether or not a juvenile male develops into a fighter mainly depends on whether it reaches a critical size threshold as a quiescent tritonymph: the immobile phase at the end of the tritonymph stage during which individuals mature into an adult. Males that are larger than the quiescent tritonymph size threshold will most likely develop into fighters, and smaller males develop into scramblers (Smallegange 2011). In line with the assumption of the ET model, male morph expression in *R. robini* is partly heritable (Radwan 2003, Smallegange and Coulson 2011). Unlike in other soil and bulb mites (e.g. *R. echinopus* and *S. berlesei*), male morph expression in *R. robini* is less affected by indicators of population density such as airborne substances (Radwan 1995) or male morph frequency (Deere and Smallegange 2014).

Survival experiments

To investigate whether tritonymphs and adults have lower survival probabilities in the presence of fighters than when alone (due to being killed by fighters), we conducted a life-stage survival experiment comprising two treatments: 1) focal life stage (four levels: tritonymph, adult female, adult scrambler and adult fighter); and 2) presence of a fighter male (two levels: yes/no). Please note that, in both survival experiments (see below), we used mobile tritonymphs and not the subsequent quiescent (immobile, 'pupating') tritonymph stage during which individuals mature. Łukasik (2010) investigated cannibalism in the related mite, *Sancassania berlesei*, and found that only fighters, and not scramblers, were able to kill juvenile and adult conspecifics. We therefore do not expect *R. robini* scramblers to be able to kill other mites, and, for that reason and for the logistical reason that another treatment will reduce the number of repeats and statistical power, refrained from running both survival experiments with presence of a scrambler male (instead of fighter male) as a control. The life-stage survival experiment followed a randomised block design whereby each week, over a period of six weeks, 7–14 individuals of each focal life stage were taken from the stock cultures and individually isolated in 12-mm diameter tubes with a plaster of Paris and moist, powdered charcoal base. No food was added. On the same day, a fighter (taken from the stock cultures) was added to half of all tubes containing individuals of each focal life stage. Survival was scored after 48 h, and the characteristics of any dead mites were recorded. Mites that are attacked by fighters appear deflated because only their exoskeleton is left; this occurs because body fluids stream out through the punctured exoskeleton of the victim and because fighters consume the body fluids. Mites that die of natural causes are typically still intact and do not deflate after being attacked by a fighter. Previous work (van den Beuken and Smallegange unpubl.) revealed no significant body size effect on the probability of being attacked within a life stage (adult females, scramblers, tritonymphs). We therefore did not measure body length, which freed up time to run more trials. The fates of 261 individuals were followed: 68 tritonymphs, 68 adult females, 67 scramblers and 58 fighters. However, at the end of these trials, in 24 cases

the focal individual or the fighter male could not be found, which left 237 trials for analysis.

The results of the first survival experiment revealed that tritonymphs in particular have a lower survival probability in the presence of fighters. In a second survival experiment, we investigated this result in more detail by investigating whether the sex ratio, expressed as the proportion of tritonymphs that mature as males, and fighter expression (proportion of male tritonymphs that mature as fighters) depend on whether or not a fighter is present with a tritonymph, i.e. we tested whether fighters might selectively kill tritonymphs of a certain sex or male morph. We also tested whether tritonymph survival depends on whether a tritonymph is alone or with a fighter, and the characteristics of any mite corpses found were recorded. The tritonymph survival experiment also followed a randomised block design, whereby over a period of nine weeks, between 8 and 37 tritonymphs (depending on how many could be found in the stock cultures) were taken from the stock culture each week and individually isolated in 12-mm diameter tubes with a plaster of Paris and moist, powdered charcoal base, without food. A fighter was added to half of the isolated tritonymphs. After 48 h (as before), fighters were removed, and the surviving focal mites were given ad libitum access to yeast. This was unlikely to affect male ART expression, because no compensatory growth has been observed in juvenile *R. robini* (Leigh and Smallegange 2014). Only after maturation can sex and male morph be determined in the bulb mite, so the mites were kept in their tubes for another 2–3 days with ad libitum access to yeast, after which the mites had matured and their sex and male morph were scored. The fates of 177 focal individuals were followed, of which 144 survived till the end of the experiment. Of those 144 trials, 12 trials had to be omitted as the fighter male was missing at the end of the experiment. In both experiments, the tubes were maintained in an unlit incubator at 25°C and $>70\%$ relative humidity.

Population experiment

The population experiment comprised three treatments: 1) harvesting of fighters (FH), 2) harvesting of scramblers (SH) and 3) no selective harvesting (control treatment, C), and was conducted from February to May 2015 (66 days) after an acclimation period of 40 days, which is sufficiently long for lab-conditioned acarid mite populations to stabilise under a constant-food regime (Cameron and Benton 2004). Although desirable, we did not conduct control treatments to control for any changes in sex ratio or total population size due to harvesting for logistical reasons. Each treatment was replicated four times, resulting in 12 experimental populations. Each population was initiated at the start of the acclimation period (40 days prior to the start of the actual experiment) with 50 randomly selected adult mites from the source population, and provided with ad libitum access to powdered yeast by providing excess yeast during both the acclimation and experimental periods. Food levels were checked every other day, and powdered yeast was added when necessary; the populations never ran out of yeast. To keep the populations in the (exponential) growth phase and prevent them from growing to carrying capacity through density-dependent competition over food, we followed the methods of Cameron and Benton (2004), where, each week, we split the populations into two by removing half of the mites (which were typically uniformly spread across the tubes). To assess that this procedure indeed kept populations in the growth phase (and hence population growth is not limited) we simulated this procedure for our population experiment using a recently developed structured population model (the dynamic energy budget integral projection model [DEB-IPM]), parameterised for *R. robini* (Smallegange et al. 2017a) (Supplementary material Appendix 1). This firstly revealed that populations quickly settle to a constant growth rate within the acclimation period of 40 days where daily population growth is always higher than unity, which is characteristic of populations that increase in size (Supplementary material Appendix 1 Fig. A1). Secondly, this showed that, each time after half the population is removed, the population recovers to its original growth rate within one-to-two days (Supplementary material Appendix 1 Fig. A1). We are therefore confident that we achieved our goal of keeping experimental populations in the growth phase by halving them each week. In the experiment, after the acclimation period, we started the selective harvesting, i.e. each week, one day after half of the population was removed (cf. Cameron and Benton 2004), the remaining eggs, juveniles (larvae, protonymphs and tritonymphs) and adults of both sexes and morphs were counted using a hand counter through a 6.5–$50\times$ stereomicroscope at $15\times$ magnification. Subsequently, harvesting was conducted by removing 50% of fighters (FH treatment) or 50% of scramblers (SH treatment). Because the DEB-IPM does not yet include male polymorphisms, we could not simulate the male morph harvesting treatments. Mite generation time varies with food supply, but under good conditions, the egg-to-egg time can be as short as 11 days (under constant temperature of 25°C) (Smallegange 2011). Even though food was available in excess, there still could have been competition for space or access to food so that harvesting lasted for maximally $66/11 = 6$ generations. The populations were fed after harvesting and maintained in 24-mm diameter, flat-bottomed glass tubes with a plaster of Paris and powdered charcoal base, which was kept moist to avoid desiccation. The tubes were sealed with a circle of very fine mesh that allowed gaseous diffusion to occur, which was held in place by the tubes' standard plastic caps with ventilation holes cut into them. The populations were maintained in an unlit incubator at 25°C and $>70\%$ relative humidity.

Predictions from the ET model are derived from functions that relate male morph fitness to a cue (Tomkins and Hazel 2007), which in the case of male bulb mites is taken to be quiescent tritonymph size (Smallegange 2011, Tomkins et al. 2011). Selection against a male morph lowers its fitness, shifting the intersection point of the fitness functions and hence the mean quiescent tritonymph size threshold from its position prior to selection to one associated with a reduced

expression of that morph. At the end of the experiment, we performed a common environment life history assay to assess whether any differences in male morph expression between treatments were due to evolutionary shifts in the mean quiescent tritonymph size threshold (cf. Smallegange and Deere 2014). Such a common environment experiment will show that, if evolutionary shifts have occurred, then descendants from the different treatment groups that are all raised in the same common environment should significantly differ in their mean quiescent tritonymph size threshold. If there are no significant differences, then any observed differences between the treatments in the population experiment are likely due to phenotypic plasticity. The common environment was started by randomly selecting five adult females from each population, individually isolated, given ad libitum access to yeast, and allowed to lay eggs for 11 days. Their offspring were followed until they reached the quiescent tritonymph stage. No adults, except the mother, were ever present among the offspring. Once quiescent tritonymphs were present, they were collected, photographed using an digital colour camera connected to a 6.5–50 × stereomicroscope, and their lengths were measured to the nearest 0.1 μm using ZEN lite imaging software (Zeiss). Subsequently, each quiescent tritonymph was individually isolated, and its sex and morph were scored after maturation the next day. Between one and four male quiescent tritonymphs per female, from a total of 23 females (we did not find quiescent tritonymph offspring in case of two females), were measured this way, resulting in a total of 37 observations. This is a low number of observations but for logistical reasons we could not measure more individuals per day. Nutrition during ontogeny is the strongest environmental determinant of male quiescent tritonymph size, and hence male morph development; the effects of maternal nutritional conditions are negligible in this species (the effect size of the offspring environment is 15-times larger than that of the maternal environment; Smallegange 2011). Therefore, rearing mites in a common environment for one generation is sufficient to eliminate any maternal effects. Females and their offspring, and all of the isolated quiescent tritonymphs, were given ad libitum access to yeast and maintained in 24-mm diameter (females and offspring) and 12-mm diameter (individual quiescent tritonymphs) tubes with a plaster of Paris and powdered charcoal base in an unlit incubator at 25°C and $>70\%$ relative humidity.

Statistical analyses

In both survival experiments, the results were only included in the analysis if, at the end of each trial, the focal mite was present (dead or alive), and if the added fighter male was alive when we scored survival. To analyse the results from the first, life-stage survival experiment, we tested the effects of the fixed factors 'focal life stage' (tritonymph, adult female, scrambler or fighter) and 'fighter presence' (yes/no) on mite survival probability, using a generalised linear mixed model (GLMM; using the *lme4* package in R, <www.r-project.org>) with a binomial response variable (1 = the focal mite survived, 0 = the focal mite died), a binomial error distribution, and 'week' as a random factor. All of the mites survived in some treatment combinations, so we were unable to test for an interactive effect of life stage and fighter presence on mite survival probability using the GLMM. We therefore used the bias reduction method of Firth (1993) implemented in the *brglm* R package (which estimates binomial-response generalised linear models (GLMs) using iterative maximum likelihood fits on binomial pseudo-data, Kosmidis 2007) to test the effect of the interaction between 'focal life stage' and 'fighter presence' on mite survival probability. This means that we excluded the random term from this analysis; to test the significance of the main effects on mite survival probability, we therefore resorted to the GLMM. For the tritonymph survival experiment, we included three response variables. Firstly, we tested the effect of the fixed factor 'fighter presence' (yes/no) on tritonymph survival probability using a GLMM with a binomial response variable (1 = the focal tritonymph survived, 0 = the focal tritonymph died), a binomial error distribution, and 'week' as a random factor. Secondly, we assessed whether the sex ratio of surviving tritonymphs (i.e. the probability that a mite matured as a male) depended on the presence of a fighter (yes/no) using a GLMM with a binomial response variable (1 = male, 0 = female), a binomial error distribution, 'fighter presence' as a fixed factor and 'week' as a random factor. We also used a two-tailed test of population proportion to assess if the observed proportion of surviving tritonymphs that matured as a male significantly deviated from the expected proportion of 0.5, assuming a 1:1 sex ratio (Oliver Jr 1977). Thirdly, we assessed whether male morph expression in the surviving tritonymphs (i.e. the probability that a male mite matured as a fighter) depended on the presence of a fighter (yes/no) using a GLMM with a binomial response variable (1 = fighter, 0 = scrambler), a binomial error distribution, 'fighter presence' as a fixed factor and 'week' as a random factor.

To analyse the results of the population experiment, we used a GLMM with Gaussian errors to analyse the effect of the fixed factor harvesting treatment (FH, SH, C), including 'measurement day' and 'population tube' as random effects to account for the repeated measures within each experimental population on: the number of eggs, the number of juveniles, the number of fighters, the number of scramblers, the number of adult females, reproductive output (by analysing treatment effects on the number of eggs with the number of adult females set as an offset so that the model prediction will be number of eggs per female), sex ratio (by analysing treatment effects on the number of adult females with the number of adult males set as an offset so that the model prediction will be number of adult females per adult male [juveniles cannot be sexed]), and the total number of individuals in each population. The model assumptions of Gaussian errors and homoscedacity were confirmed by inspecting the probability plots and error structures. We used a GLMM with binomial errors to analyse the effect of the fixed factor harvesting treatment (FH, SH, C), including 'measurement day'

and 'population tube' as random effects, on the proportion of males that were fighters.

To analyse the results of the life history assay conducted at the end of the population experiment, we used a GLMM with Gaussian errors to analyse the effects of harvesting treatment, male morph and its interaction on quiescent tritonymph size (μm). The model assumptions of Gaussian errors and homoscedacity were confirmed by inspecting the probability plots and error structures. We used a GLMM with binomial errors to analyse the effects of harvesting treatment and quiescent tritonymph size on male morph expression (0 if scrambler, 1 if fighter) (cf. Tomkins et al. 2011). In each GLMM, 'maternal identity' and 'population tube' were included as random terms, and the significance of the treatment effects was tested using a model simplification procedure, whereby the full model was fitted after the least significant term had been removed, if the deletion caused an insignificant increase in deviance as assessed by a maximum likelihood ratio test. Pairwise comparisons among the three different harvesting levels were conducted by creating a reduced model within which two levels were combined. If the reduced model caused an insignificant increase in deviance as assessed by a maximum likelihood ratio test ($\alpha = 0.05$), then the two levels were considered to be not significantly different. All of the analyses were conducted in R and for all GLMMs we used the *lme4* package (<www-r-project.org>).

Data deposition

Data available from FigShare: <https://figshare.com/s/9d3bbbd1b26e0a5cb6e2> (Smallegange et al. 2017b).

Results

Survival experiments

The GLM (using the bias-reduction method) revealed no significant effect of the interaction between fighter presence and life stage ($z = 0.787$, $p = 0.431$), although visual inspection revealed that the reduction in mean survival probability when a fighter is present tended to be larger for tritonymphs than for other life stages (Fig. 1: pairwise dashed versus open bars). Continuing with the GLMM, we did find a significant effect of fighter presence on overall survival probability (GLMM: $z = -3.382$, $p < 0.001$, $n = 237$). When alone, nearly all of the mites survived, and their average survival probability was 0.98 ± 0.001 SE (standard error) ($n = 119$). In the presence of fighters, the average survival probability was significantly lower, and averaged across all four life stages it equalled 0.82 ± 0.003 SE ($n = 118$). Except for one individual, all of the individuals that had died in the presence of a fighter had their cuticles punctured, so that only deflated exoskeletons remained, indicating that these individuals were killed by fighters. We also found significant differences among the life stages in average survival probability (Fig. 1, grey bars): on average, the tritonymph survival probability was significantly lower than the female survival probability ($z = -2.631$, $p = 0.009$), and marginally, non-significantly lower than the scrambler survival probability ($z = -1.765$, $p = 0.078$). Differences in survival probability between the other pairwise life-stage combinations were all non-significant (tritonymph versus fighter: $z = 1.438$, $p = 0.151$; scrambler versus fighter: $z = -0.169$, $p = 0.866$; scrambler versus female: $z = 1.230$, $p = 0.219$; fighter versus female: $z = 1.317$, $p = 0.189$) (Fig. 1, grey bars).

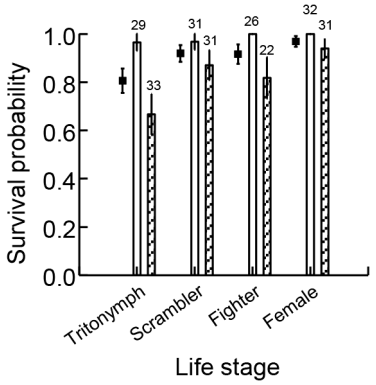

Figure 1. Survival probability of mites at different life stages recorded in the first survival experiment. Black squares denote the mean survival probability of each life stage; for each life stage, bars denote the survival probability of mites alone (open bars) and in the presence of a fighter male (dashed bars). Vertical lines are standard errors; no standard errors are shown for females and fighters that were alone, as in both cases, all of the individuals survived. Numbers above bars denote sample sizes.

We further investigated the tritonymph survival probability in the second survival experiment. Firstly, we found that the tritonymph survival probability was significantly lower in the presence of a fighter ($z = -2.346$, $p < 0.001$, $n = 132$) (Table 1); again, all of the tritonymphs that had died in the presence of a fighter had their cuticles punctured, so only deflated exoskeletons remained, indicating that they were killed by armed fighters. Next, we tested whether fighter expression and sex ratio after maturation depended on whether or not a fighter was present with the tritonymph. The presence of a fighter decreased the probability that a male tritonymph matured as a fighter ($z = -1.970$, $p = 0.049$, $n = 56$) (Table 1). This result did not carry over to affect the sex ratio, as the presence of a fighter had no significant effect on the probability that mites emerged as males ($z = -0.981$, $p = 0.327$, $n = 132$) (Table 1). However, the two-tailed test of population proportion revealed that the lack of a significant effect of fighter presence on sex ratio was probably caused by low statistical power. When a tritonymph was alone, the proportion of males emerging was not significantly different to an equal sex ratio of 0.5 $\left[z = (0.50 - 0.46) \big/ \sqrt{0.5 \times (0.5/76)} = 0.697; \; p = 0.486 \right]$ (Table 1), but when a fighter was present, the proportion of males emerging tended to be much lower than the expected, equal sex ratio of 0.5 (Oliver Jr 1977) $\left[z = (0.50 - 0.38) \big/ \sqrt{0.5 \times (0.5/56)} = 1.796; \; p = 0.072 \right]$ (Table 1).

Table 1. Results of the second survival experiment, showing the mean with standard error (SE) of each of the three response variables, depending on whether a fighter male was either present or absent: 1) tritonymph survival probability, 2) the proportion of males that matured as fighters, and 3) the proportion of adults that matured as males.

	Response variable		
Fighter present?	Survival probability	Proportion fighter males	Proportion male adults
No	0.96 ± 0.002 SE (n = 76)	0.86 ± 0.01 SE (n = 35)	0.46 ± 0.007 SE (n = 76)
Yes	0.67 ± 0.005 SE (n = 56)	0.62 ± 0.02 SE (n = 21)	0.38 ± 0.009 SE (n = 56)

Population experiment

Time series of the average numbers of eggs, juveniles and adults observed in each treatment are presented in Fig. 2A–C. Figure 2D–E shows the mean number of adult females, scramblers and fighters. Unexpectedly, the number of fighters was significantly higher in the fighter-harvesting (FH) treatment than in the SH treatment (FH versus SH: $t = 3.079$, $p = 0.003$) and significantly higher in the FH than in the C treatment (FH versus C: $t = 4.411$, $p < 0.001$) (fighter number did not differ between the C and SH treatments: $t = -1.297$, $p = 0.197$) (Fig. 3A). The significant difference in fighter numbers between the fighter and scrambler harvesting treatment carried over to affect fighter expression (SH versus FH: $z = 2.543$, $p = 0.011$), but fighter expression did not differ significantly within the other treatment combinations (C versus FH: $z = 1.793$, $p = 0.073$; C versus SH: $z = -0.626$, $p = 0.531$) (Fig. 3B). The significant differences in fighter numbers between the FH and C treatments also carried over to affect the female-to-male sex ratio, which was significantly higher in the FH than in the C treatment (C versus FH: $t = -2.669$, $p = 0.009$) but did not differ significantly between the SH and C treatments, or SH and FH treatments (C versus SH: $t = -0.773$, $p = 0.441$; SH versus FH: $t = -1.870$, $p = 0.064$) (Fig. 3C). Since there were no significant treatment effects on the number of adult females (C versus FH: $t = 1.025$, $p = 0.307$; C versus SH: $t = 0.460$, $p = 0.646$; SH versus FH: $t = 0.552$, $p = 0.582$) (Fig. 3D), the significant differences in sex ratio between the FH than in the C treatment is therefore most likely driven by the significant variation in the number of fighters (Fig. 3A). There were no significant differences among the treatments in the number of scramblers (C versus FH: $t = 1.030$, $p = 0.305$; C versus SH: $t = 1.601$, $p = 0.112$; SH versus FH: $t = 0.573$, $p = 0.568$: Fig. 3E), the number of eggs (C versus FH: $t = 0.543$, $p = 0.588$; C versus SH: $t = -1.267$, $p = 0.208$; SH versus FH: $t = -1.809$, $p = 0.073$: Fig. 3F), the number of juveniles (C versus FH: $t = 0.501$, $p = 0.617$; C versus SH: $t = 0.773$, $p = 0.441$; SH versus FH: $t = 0.276$, $p = 0.783$: Fig. 3G), reproductive output

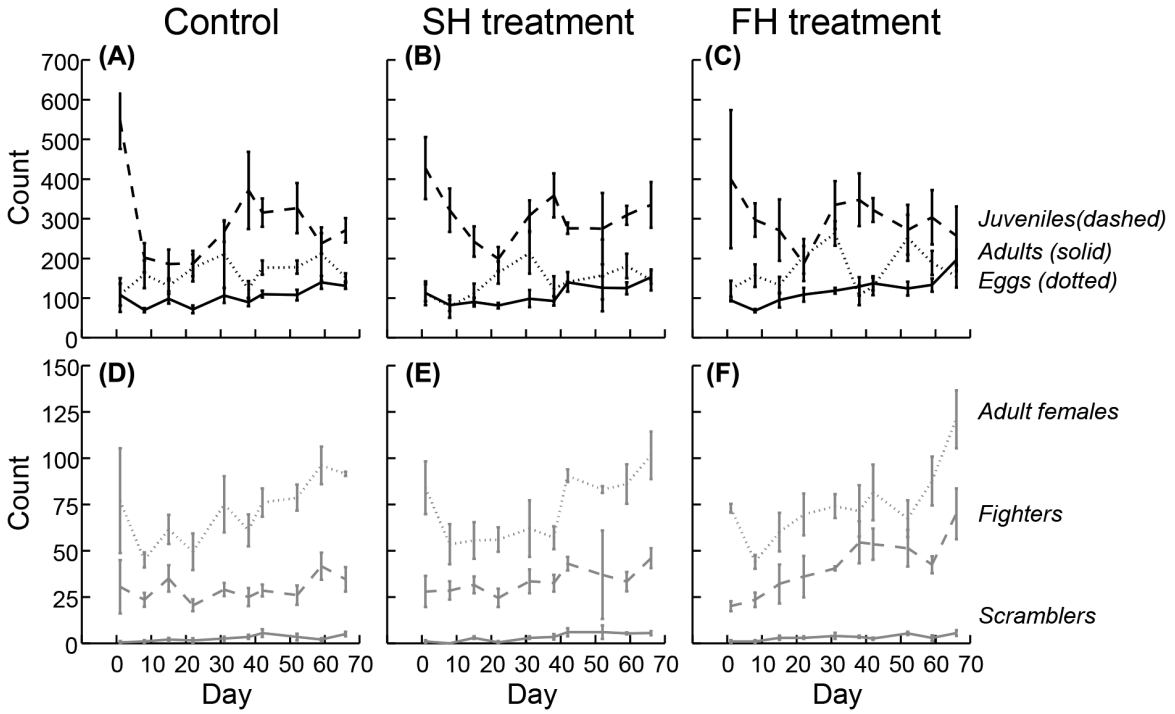

Figure 2. Time series averaged for control (A, D), scrambler-harvesting (SH) (B, E) and fighter-harvesting (FH) treatments (C, F). The top panels show the mean numbers of adults (solid lines), eggs (dotted lines) and juveniles (dashed lines); the bottom panels show in grey the mean numbers of individuals in each of the adult life stages: fighters (dashed lines), scramblers (solid lines) and females (dotted lines). Each treatment was replicated four times, resulting in 12 experimental populations.

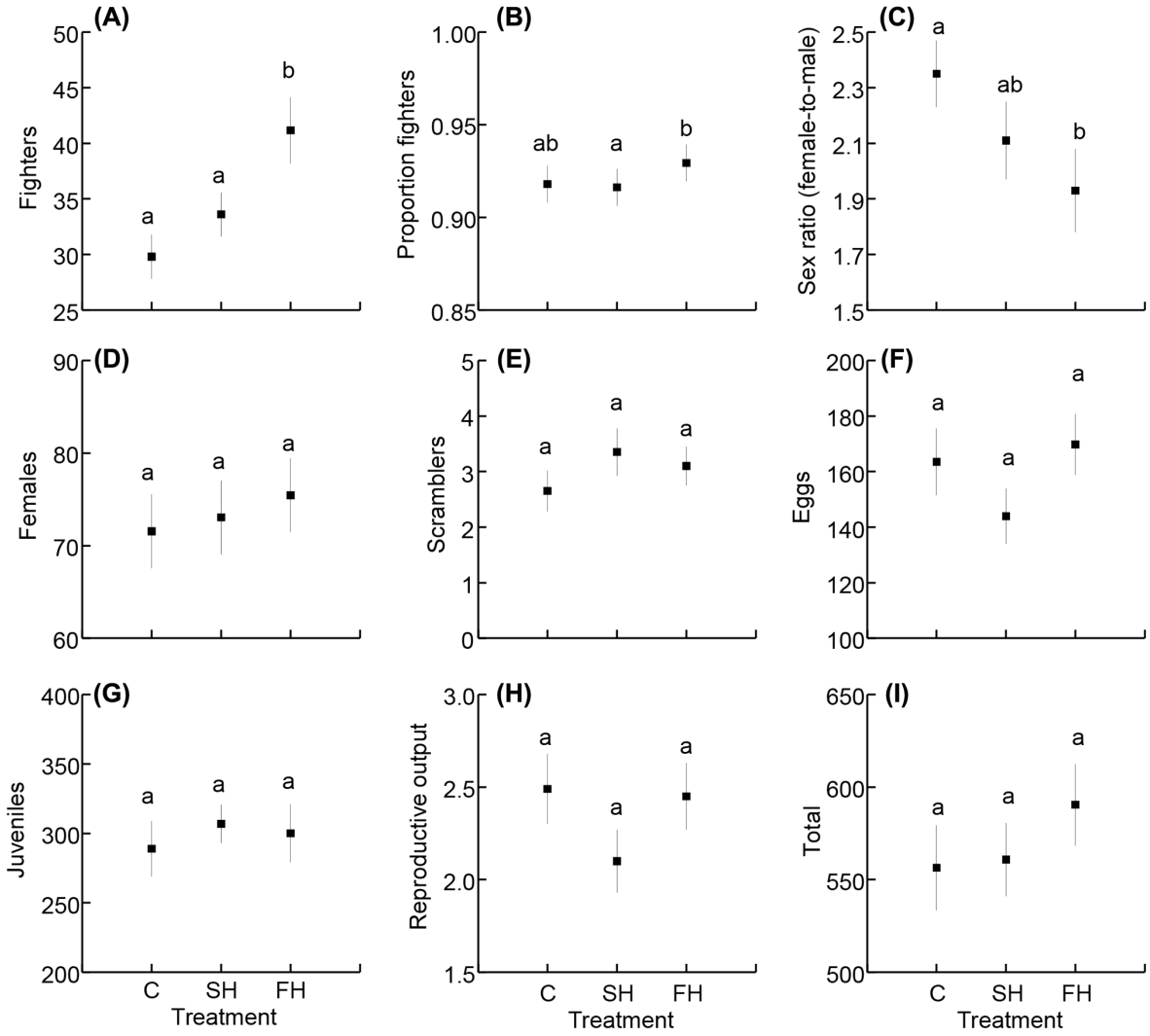

Figure 3. Mean number of fighters (A), proportion of males that were fighters (B), adult female-to-adult male sex ratio (C), number of adult females (D), number of scramblers (E) number of eggs, (F), number of juveniles (G), reproductive output (number of eggs divided over the number of adult females) (H) and the mean total number of individuals (**I**) per treatment group, averaged over the experimental period (Fig. 2). C – control; SH – scrambler harvesting; FH – fighter harvesting. The black squares are the observed means across replicate populations and the vertical lines are standard errors of the mean. Letters above the means in each panel denote whether treatments had a significant effect on each response variable at $\alpha = 0.05$. Each treatment was replicated four times, resulting in 12 experimental populations, which structure and size was scored ten times over a period of 66 days.

(C versus FH: $t = -0.213$, $p = 0.832$; C versus SH: $t = -1.438$, $p = 0.153$; SH versus FH: $t = 1.653$, $p = 0.101$: Fig. 3H), or the total number of individuals (C versus FH: $t = 1.393$, $p = 0.166$; C versus SH: $t = 0.254$, $p = 0.800$; SH versus FH: $t = 1.122$, $p = 0.264$: Fig. 3I).

The life history assay conducted at the end of the experiment revealed that fighter expression did not significantly differ among the treatments ($\chi^2_2 = 0.014$, $p = 0.993$). Averaged across all of the treatments, the probability of fighter expression was 0.86 ± 0.06 SE; this was not significantly different to the probability of fighter expression in the second survival experiment (0.86 ± 0.01 SE). Quiescent tritonymph size did not significantly affect the probability of fighter expression ($\chi^2_1 = 0.091$, $p = 0.763$), probably because most males emerged as fighters ($n = 32$) and only a few as scramblers ($n = 5$). As a result, the statistical power was probably too low to assess the mean quiescent tritonymph size threshold for male morph expression. We did not find a significant effect of the interaction between treatment and male morph on quiescent tritonymph size ($\chi^2_2 = 0.11$, $p = 0.741$). We also found that quiescent tritonymph size did not significantly differ between the two male morphs ($\chi^2_2 = 1.43$, $p = 0.232$): on average, fighter quiescent tritonymphs were 597.6 μm ± 7.6 SE long and scrambler quiescent tritonymphs were 565.9 μm ± 14.4 SE long. To check whether this lack of a significant result could have been caused by low statistical power, we calculated Cohen's effect size d (Cohen 1988) as $d = (\bar{x}_1 - \bar{x}_2)/s$, with $\bar{x}_1$ and $\bar{x}_2$ as the mean quiescent tritonymph sizes of

fighters and scramblers, respectively, and with s as the pooled standard deviation: $s = \sqrt{[(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2]/(n_1 + n_2)}$. This revealed a large effect size of $d = 0.78$ ($n_1 = 32; n_2 = 5$). From this we infer that re-running the experiment with more replicates could confirm previous results that fighter quiescent tritonymphs are significantly longer than scrambler quiescent tritonymphs (Smallegange 2011). Finally, we found a marginally non-significant effect of harvesting treatment on quiescent tritonymph size ($\chi_2^2 = 5.25$, $p = 0.072$): on average, quiescent tritonymphs were 588.4 μm ± 11.8 SE long in the control treatment, 613.8 μm ± 9.5 SE long in the FH treatment and 563.5 μm ± 12.1 SE long in the SH treatment. An important assumption of the conditional expression of size-dependent ARTs is that if the body length distribution changes location (e.g. mean body length becomes smaller), then the mean tritonymph length threshold for morph expression evolves such that its new location is at the same (relative) position within the body length distribution as before the change in mean body length (Tomkins et al. 2011). Therefore, any effect on body length distributions by other, unknown factors would result in different shifts in mean tritonymph length thresholds between treatments, because the threshold will track each change in body length distribution within each treatment, all else being equal. If harvesting had the exact opposite effect, then both types of effect would cancel each other out, resulting in an apparent lack of a harvesting treatment effect. Although this scenario is unlikely to have occurred in our experiment, we repeated the fighter expression analysis with each individual's quiescent tritonymph length standardized as a deviation from the mean length within its treatment (cf. Tomkins et al. 2011). The results of this analysis confirmed our initial results: neither treatment ($\chi_1^2 = 0.055$, $p = 0.973$) nor standardised quiescent tritonymph size ($\chi_1^2 = 0.050$, $p = 0.823$) significantly affected fighter expression.

Discussion

Individual heterogeneity in life histories plays an important role in the ecological and evolutionary processes that occur within populations (Smallegange and Coulson 2013, Vindenes and Langangen 2015), but unravelling the underlying mechanisms that shape the resulting population fluctuations can be challenging (Smallegange and Deere 2014). Here, we investigated how individual heterogeneity in ARTs determines fluctuations in experimental populations of *Rhizoglyphus robini*. In a previous experiment using this species, we found that the selective harvesting of scramblers counterintuitively decreased (instead of increased) fighter frequency (Smallegange and Deere 2014). Smallegange and Deere (2014) hypothesised that the harvesting of scramblers deprived fighters of scrambler 'prey', resulting in an evolutionary shift towards reduced fighter expression. However, the results from this study, particularly the fact that fighters preferentially killed juveniles, suggests that this hypothesis was premature and alternative explanations could be equally valid such as 1) removing scramblers results in cryptic selection against fighters, 2) removing scramblers reduces competition of food between adult scramblers and juveniles so that more juveniles mature, affecting male morph expression, or 3) removing scramblers reduces genetic variation in the size threshold for male morph expression, thereby selecting against fighters. In this study, we tested the hypothesis that, in the absence of ecological feedback mechanisms resulting from strong density-dependent competition over food, selection against scramblers (or fighters) would decrease scrambler (or fighter) frequency and increase fighter (or scrambler) frequency through an evolutionary shift in the threshold for male morph expression. We found that the selective harvesting of scramblers had no significant effect on scrambler frequency, and neither did we find an evolutionary shift in the size threshold for male morph expression. It should be noted, however, that male morph expression in the current population experiment was highly biased towards fighters from the start: on average, of all the adult males in the control populations, less than 10% were scramblers. In comparison, male morph expression in our previous study was biased towards scramblers as about 80% of males were scramblers at the start of the experiment (Smallegange and Deere 2014: Fig. 4.2). To elicit an evolutionary shift in scrambler expression that is already very low at the start of the scrambler harvesting treatment, is likely a futile exercise and we therefore refrain from interpreting and discussing the effects of scrambler harvesting in our population experiment. The harvesting of fighters, in contrast, did affect population structure in our population experiment. Rather surprisingly, fighter expression was significantly higher in the fighter-harvesting treatment than in the control treatment. We did not find evidence in the life history assay that we conducted at the end of the population experiment to support that this shift in fighter expression was the result of an evolutionary shift in the size threshold for male morph expression. It is possible that six generations of selective harvesting was insufficient to elicit an evolutionary response. For example, in our previous study, our harvesting frequency was just under five times per generation (Smallegange and Deere 2014), whereas in this study, our harvesting frequency was just under twice per generation. Also, Radwan (2003), found a significant response over six generations in only one out of the two discrete-generation experiments on male morph expression in *R. robini* that he conducted. Although, in our own discrete-generation experiment, we did find a strong evolutionary response in male morph expression over only five generations of selectively harvesting fighters under ad libitum food conditions (Smallegange and Coulson 2011). Regardless of the fact that we did not find an evolutionary shift in male morph expression, be it due to the short duration of the experiment, or genuine lack of evolutionary shift, the increase in fighter numbers in the fighter-harvested populations compared to the control populations requires

explaining. Given the lack of empirical evidence of an evolutionary shift in the threshold for male morph expression, we consider this increase in fighter numbers in response to the selective harvesting of fighters to be an ecological change in population structure. This means that this response is best characterised as an overcompensatory response to the selective harvesting of fighters (Schröder et al. 2014). It could even have been possible that this overcompensatory response counteracted any evolutionary shift in the threshold for male morph expression. The question now is to identify the underlying mechanism that drives this overcompensatory response in fighter number in response to fighter harvesting.

Overcompensation is a term that is used to describe a process in which mortality imposed on a (part of a) population or species can, counterintuitively, increase the density of a specific life stage, the total population density or the density of another species (Cameron and Benton 2004, Ohlberger et al. 2011, Schröder et al. 2014). In many cases, overcompensation is driven by a change in the form or strength of density-dependence, so that a life stage, population or species (temporarily) experiences reduced competition over food, for example (de Roos and Persson 2013). In our experiment, the overcompensatory response in fighters could have been due to females producing more male eggs in response to the consistent removal of males from the population. However, females did not significantly increase their reproductive output in the fighter harvesting treatment compared to the other treatments. Given the fact that in *R. robini*, sex determination is of the XO-type (Oliver Jr 1977), it is therefore highly unlikely that the overcompensatory response in fighter numbers is driven by differential female reproductive output. A second possible explanation is that the removal of fighters reduced the attack rate by fighters on male juveniles (as fighter preferentially attacked male tritonymphs in our survival experiments) so that more males survived till adulthood. This preferential killing of male juveniles is likely not to obtain nutrients, but to reduce male–male competition by removing male competitors from the population (Radwan et al. 2000). By removing adult fighters, more male juveniles survive to adulthood, which would lead to an increase in both scrambler and fighter numbers. However, because the number of scramblers in our population experiment was very low (and any harvesting effects on scrambler numbers could not be detected), effects of the increased survival of male juveniles through fighter harvesting could only be reflected in an increase in fighter numbers. However, we also observed in our second survival experiment that the proportion of fighters that emerged from male final instars was significantly lower in the presence of a fighter than when alone. A third explanation for the overcompensatory response in fighter numbers is therefore that adult fighters preferentially kill immature fighters. By targeting the final instar stage of rival fighter males that have not yet developed their fighter weaponry, adult fighters minimise the risk of wounding or death. If either of the two latter explanations were true, this raises the question of how adult fighters recognise which final instars will mature as males, or, more intriguingly, which final instars will mature as fighters? Scrambler final instars could, for example, not be recognised as such, so that fighters cannot discriminate between scrambler and female final instars. Such a lack of sneaker (scrambler) discrimination has been observed in the spider mite *Tetranychus urticae*. In this species, males plastically adopt one of three ARTs to be the first to mate with a virgin female (the first mating ensures the paternity of most offspring, Helle 1967): opportunistic males continuously search for virgin females; fighter males guard female final instars and aggressively chase away rival males; or sneaker males guard (mount) female final instars but do not chase away rivals, and, crucially, neither are they chased away by other males (Sato et al. 2013). Male spider mites can respond to sex pheromones released by females via olfactory cues (Margolies and Collins 1994), which led Sato et al. (2013) to hypothesise that sneaker males might mimic the odour of a female (e.g. pheromone) and thereby go unnoticed by rival males. The same mechanism could explain why scrambler final instars in our experiments were not as likely to be killed by adult fighters as were fighter final instars; fighter final instars might not be able to mimic the odour of a female final instar. Female mimicry is a well-known alternative to the fighter tactic to gain access to females, and occurs in a wide range of taxa (Shuster and Wade 1991, Oliveira et al. 2008, Küpper et al. 2016). Whether scrambler males adopt a female mimic tactic in the bulb mite remains to be confirmed, but this hypothesis would explain why fighters and scramblers coexist in the bulb mite, as the benefits associated with the fighter tactic appear to greatly outweigh those associated with the sneaker tactic (Radwan et al. 2000, Radwan and Klimas 2001, Radwan 2007, Smallegange and Johansson 2014).

The unexpected responses to selective ART harvesting that we observed in this and a previous study (Smallegange and Deere 2014) beg the question in what other ways individual heterogeneity in ARTs could affect the eco-evolutionary dynamics of populations? Recently, using field data, Weir et al. (2016) postulated that ARTs can shape the evolution of body size and affect sexual size dimorphism; however, the eco-evolutionary population consequences of the interaction between such different types of individual heterogeneity remain unexplored. Vindenes and Langangen (2015) recently used integral projection models (Easterling et al. 2000) to develop a demographic framework that links individual life histories and population-level processes, and that can incorporate interactions between different types of individual heterogeneity. The authors concluded that individual heterogeneity cannot be ignored when studying the mechanisms of eco-evolutionary population dynamics, because predictions of population biology parameters depend upon whether or not individual heterogeneity is included (Vindenes and Langangen 2015). Apart from influencing body size distributions and sexual size dimorphism, ART expression is related to the process of dispersal in many species. Lawrence (1987) demonstrated that sneaker milkweed beetles *Tetraopes tetraophthalmus* disperse more often from male-biased populations

than do fighters in order to avoid male–male competition. As a result, sneakers that have dispersed obtain more matings on average than non-dispersing sneakers (Lawrence 1987). *Rhizoglyphus robini* can develop into a distinct disperser life stage in response to adverse environmental conditions, and can disperse long distances via phoresy (Houck and O'Connor 1991). We did not observe any dispersers in this study, probably because the mites were under favourable environmental conditions. However, when bulb mites do develop into this stage during ontogeny, males always mature as fighters (Deere et al. 2015). Therefore, newly founded populations might be fighter-biased, with all its associated ecological and evolutionary population consequences. Even more extreme cases occur in many species of fig wasp, in which males are either winged and always move away from their natal fig fruit to mate or small and wingless and mate within their natal fig fruit (Cook et al. 1997). Based on an extensive analysis of an integral projection model that describes the population dynamics of grey wolves *Canis lupus*, Coulson et al. (2011) concluded that accurate predictions of eco-evolutionary population dynamics are unlikely to be possible. However, the ongoing development of demographic frameworks that include more biological realism, such as dispersal (Hanski and Mononen 2011), individual heterogeneity (Vindenes and Langangen 2015), energy budgets (Smallegange et al. 2017a), and genetic structure (Coulson et al. 2016), combined with new insights from experimental and field studies into the mechanisms of eco-evolutionary change (this issue), should ensure that eventually we will be able to accurately predict the fate of populations (Clements and Ozgul 2016).

Acknowledgements – We thank the Population Biology group at IBED for valuable feedback.
Funding – IMS is funded by a MacGillavry Fellowship from the University of Amsterdam, and MEERVOUD (no. 836.13.001) and VIDI (no. 864.13.005) grants from the Netherlands Organisation for Scientific Research (NWO).

References

Cameron, T. C. and Benton, T. G. 2004. Stage-structured harvesting and its effects: an empirical investigation using soil mites. – J. Anim. Ecol. 73: 966–1006.
Cameron, T. C. et al. 2013. Eco-evolutionary dynamics in response to selection on life-history. – Ecol. Lett. 16: 754–763.
Clements, C. F. and Ozgul, A. 2016. Including trait-based early warning signals helps predict population collapse. – Nat. Commun. 7: 10984.
Cohen, J. 1988. Statistical power analysis for the behavioral sciences, 2nd edn. – Lawrence Earlbaum Assoc.
Cook, J. M. et al. 1997. Alternative mating tactics and extreme male dimorphism in fig wasps. – Proc. Biol. Sci. 264: 747–754.
Coulson, T. et al. 2011. Modeling effects of environmental change on wolf population dynamics, trait evolution and life history. – Science 334: 1275–1278.
Coulson, T. et al. 2016. Quantitative genetics meets integral projection models: unification of widely used methods from ecology and evolution. – arXiv:1509.01351.
de Roos, A. M. and Persson, L. 2013. Population and community ecology of ontogenetic development. – Princeton Univ. Press.
Deere, J. A. and Smallegange, I. M. 2014. Does frequency-dependence determine male morph survival in the bulb mite *Rhizoglyphus robini*? – Exp. Appl. Acarol. 62: 425–436.
Deere, J. A. et al. 2015. Life history consequences of the facultative expression of a dispersal life stage in the phoretic bulb mite (*Rhizoglyphus robini*). – PLoS One 10: e0136872.
Díaz, A. et al. 2000. Biology, ecology and management of the bulb mites of the genus *Rhizoglyphus* (Acari: Acaridae). – Exp. Appl. Acarol. 24: 85–113.
Easterling, M. R. et al. 2000. Size-specific sensitivity: applying a new structured population model. – Ecology 81: 694–708.
Firth, D. 1993. Bias reduction of maximum likelihood estimates. – Biometrika 80: 27–38.
Gross, M. R. 1991. Salmon breeding behavior and life history evolution in changing environments. – Ecology 72: 1180–1186.
Hanski, I. and Mononen, T. 2011. Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. – Ecol. Lett. 14: 1025–1034.
Hazel, W. N. et al. 1990. A polygenic model for the evolution and maintenance of conditional strategies. – Proc. Biol. Sci. 242: 181–187.
Hazel, W. N. et al. 2004. The ecological genetics of conditional strategies. – Am. Nat. 163: 888–900.
Helle, W. 1967. Fertilization in the two-spotted spider mite (*Tetranychus urticae*: Acari). – Entomol. Exp. Appl. 10: 103e110.
Houck, M. A. and O'Connor, B. M. 1991. Ecological and evolutionary significance of phoresy in the Astigmata. – Annu. Rev. Entomol. 36: 611–636.
Kolss, M. et al. 2009. Life history consequences of adaptation to larval nutritional stress in *Drosophila*. – Evolution 63: 2389–2401.
Kosmidis, I. 2007. Bias reduction in exponential family nonlinear models. – PhD thesis, Dept of Statistics, Univ. of Warwick <www.ucl.ac.uk/~ucakiko/files/ikosmidis_thesis.pdf>.
Kotiaho, J. S. et al. 2003. Males influence maternal effects that promote sexual selection: a quantitative genetic experiment with dung beetles *Onthophagus taurus*. – Am. Nat. 161: 852–859.
Küpper, C. et al. 2016. A supergene determines highly divergent male reproductive morphs in the ruff. – Nat. Genet. 48: 79–83.
Lawrence, W. S. 1987. Dispersal: an alternative mating tactic conditional on sex ratio and body size. – Behav. Ecol. Sociobiol. 21: 367–373.
Leigh, D. M. and Smallegange, I. M. 2014. Effects of variation in nutrition on male morph development in the bulb mite *Rhizoglyphus robini*. – Exp. Appl. Acarol. 64: 159–170.
Łukasik, P. 2010. Trophic dimorphism in alternative male reproductive morphs of the acarid mite *Sancassania berlesei*. – Behav. Ecol. 21: 270–274.
Margolies, D. C. and Collins, R. D. 1994. Chemically-mediated pre-mating behavior in two tetranychid species. – Exp. Appl. Acarol. 18: 493–501.
Ohlberger, J. et al. 2011. Stage-specific biomass overcompensation by juveniles in response to increased adult mortality in a wild fish population. – Ecology 92: 2175–2182.

Oliveira, R. F. et al. 2008. Alternative reproductive tactics. – Cambridge Univ. Press.
Oliver Jr, J. H. 1977. Cytogenetics of mites and ticks. – Annu. Rev. Entomol. 22: 407–429.
Radwan, J. 1995. Male morph determination in two species of acarid mites. – Heredity 74: 669–673.
Radwan, J. 2003. Heritability of male morph in the bulb mite, *Rhizoglyphus robini* (Astigmata, Acaridae). – Exp. Appl. Acarol. 29: 109–114.
Radwan, J. 2007. Sexual selection and conflict in the bulb mite, *Rhizoglyphus robini* (Astigmata: Acaridae). – Exp. Appl. Acarol. 42:151–158.
Radwan, J. 2009. Alternative mating tactics in acarid mites. – Adv. Stud. Behav. 39: 185–208.
Radwan, J. and Klimas, M. 2001. Male dimorphism in the bulb mite, *Rhizoglyphus robini*: fighters survive better. – Ethol. Ecol. Evol. 13: 69–79.
Radwan, J. et al. 2000. Aggressiveness in two male morphs of the bulb mite *Rhizoglyphus robini*. – Ethology 106: 53–62.
Roff, D. A. 1996. The evolution of threshold traits in animals. – Q. Rev. Biol. 71: 3–35.
Santos, M. et al. 1997. Density-dependent natural selection in *Drosophila*: evolution of growth rate and body size. – Evolution 51: 420–432.
Sato, Y. et al. 2013. Alternative phenotypes of male mating behaviour in the two-spotted spider mite. – Exp. Appl. Acarol. 61: 31e41.
Schoener, T. W. 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. – Science 331: 426–429.
Schröder, A. et al. 2014. When less is more: positive population-level effects of mortality. – Trends Ecol. Evol. 29: 614–624.
Shuster, S. M. and Wade, M. J. 1991. Equal mating success among male reproductive strategies in a marine isopod. – Nature 350: 608–610.
Smallegange, I. M. 2011. Complex environmental effects on the expression of alternative reproductive phenotypes in the bulb mite. – Evol. Ecol. 25: 857–873.
Smallegange, I. M. and Coulson, T. 2011. The stochastic demography of two coexisting male morphs. – Ecology 92: 755–764.
Smallegange, I. M. and Coulson, T. 2013. Towards a general, population-level understanding of eco-evolutionary change. – Trends Ecol. Evol. 28: 143–148.
Smallegange, I. M. and Deere, J. A. 2014. Eco-evolutionary interactions as a consequence of selection on a secondary sexual trait. – Adv. Ecol. Res. 50: 145–169.
Smallegange, I. M. and Johansson, J. 2014. Life history differences favor evolution of male dimorphism in competitive games. – Am. Nat. 183: 188–198.
Smallegange, I. M. et al. 2017a. Mechanistic understanding of population dynamics using dynamic energy budget theory incorporated into integral projection models. – Methods Ecol. Evol. 8: 146–154.
Smallegange, I. M. et al. 2017b. Data from: Population consequences of individual heterogeneity in life histories: overcompensation in response to harvesting of alternative reproductive tactics. – FigShare <https://figshare.com/s/9d3bbbd1b26e0a5cb6e2>.
Tomkins, J. L. and Hazel, W. 2007. The status of the conditional evolutionarily stable strategy. – Trends Ecol. Evol. 22: 522–528.
Tomkins, J. L. et al. 2011. Habitat complexity drives experimental evolution of a conditionally expressed secondary sexual trait. – Curr. Biol. 21: 569–573.
Vindenes, Y. and Langangen, Ø. 2015. Individual heterogeneity in life histories and eco-evolutionary dynamics. – Ecol. Lett. 18: 417–432.
Weir, L. K. et al. 2016. Sneaker males affect fighter male body size and sexual size dimorphism in salmon. – Am. Nat. 188: 264–271.

Supplementary material (available online as appendix oik-04130 at <www.oikosjournal.org/appendix/oik-04130>). Appendix 1.