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Evolution of developmental plasticity and the potential of host shift in the seed beetle: Insights from laboratory evolution experiments

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Abstract

1. Expansion of the host range in phytophagous insects, followed by the specialisation on novel hosts, encompasses changes in many aspects of insects' behaviour, physiology, and the interaction between their life-history features.
2. Here, we analyse the roles of insects' developmental plasticity in the process of host shift. Using laboratory populations of the seed beetle (*Acanthoscelides obtectus*), which have evolved on both optimal (common beans) and suboptimal (chickpea) plant hosts for more than 35 years, we experimentally replicated the process of host shift and analysed the patterns of short-term and long-term life-history responses to host variation.
3. In order to test whether selection for increased plasticity has an effect on host shifting processes, we used existing bean and chickpea adapted populations to establish new populations in which the host plant offered for insect development was changed each generation (for 13 generations). To test the potential for a short-term plastic response, beetles from each laboratory population were raised on both hosts for one generation.
4. Results showed that, in contrast to the populations that evolved on beans, which maintained high levels of developmental plasticity, long-term host switching to chickpeas was accompanied with specialisation of pre-adult viability with a simultaneous increase in fecundity. Populations evolved on alternate plant hosts that revealed similar plasticity patterns as their ancestral populations.
5. These results suggest that short-term plastic responses could determine the paths of long-term evolution of life-history plasticity. However, more time could be needed for plasticity to evolve differently from the initial responses.

KEYWORDS
Acanthoscelides obtectus, experimental evolution, host shift, life-history traits, phenotypic plasticity, seed beetle

INTRODUCTION

Insects that are capable of digesting and metabolising many plant species from diverse plant families are known as generalists (Rafter & Walter, 2020). Using multiple food sources and exploiting different resources could indeed have obvious ecological and evolutionary advantages. However, the majority of phytophagous insect species, including economically relevant ones, fall into the category of host plant specialists that use one plant, or several species from the same plant family, in their diets (Futuyma & Agrawal, 2009; Schoonhoven et al., 2005). Considering the abundance of plant specialists in nature, it seems that such a strategy must be beneficial for insects (Bernays & Graham, 1988). One of the most common explanations assumes that only specialists can be efficient enough in handling plants' defences and successful detoxification of their chemical components (Ali & Agrawal, 2012; Forister et al., 2015; Hagstrum & Subramanyam, 2009). If the pattern of plant defences is recurring, an insect can constitutively invest in countermeasures or even use them as oviposition or feeding stimulants (Heckel, 2014).

Importantly, there are indications that even a specialist can expand its host range, exploit alternative food sources, and then specialise in a novel host plant. This concept is known as the oscillation hypothesis (Janz & Nylin, 2008; Nylin et al., 2014). This host shift process can be very challenging to diverse aspects of insects' behaviour (Martinossi-Allibert et al., 2018; Wink, 2018), physiology, including digestive enzymes, and detoxifying processes (War et al., 2018), morphology (de Sousa-Lopes et al., 2022), and the relationship between life-history traits (Messina et al., 2009). Crucial for successful host shift is the process of adaptive phenotypic plasticity, which is defined as the ability of insect individuals to receive external signals from a novel host and develop a phenotype that is appropriate to deal with the chemical and physical characteristics of a new plant host (Forsman, 2015). This step in the host shift has the potential to influence long-term (evolutionary) modes of population's change and allow survival and stable population growth under new conditions (Savković et al., 2016, 2019). As a consequence, a population exposed to a new environment could be able to experience considerable change in the evolutionary trajectories of individual physiology, morphology, and life-history strategies (Saeki et al., 2014).

The epistasis model of plasticity (Scheiner & Lyman, 1991) recognises that loci responsible for the plasticity of a trait can differ from loci involved in the determination of the trait itself. Consequently, plasticity per se can evolve independently from the mean value of the specific trait, that is, by having its own genetic background, plasticity as a trait can have an evolutionary path that is independent of the trait itself. Furthermore, if plasticity is observed as an independent trait, it is expected that populations would demonstrate different levels of genetic variation for plasticity. Under such circumstances, natural selection can promote diversification and the evolution of plasticity (Lafuente & Beldade, 2019; Pigliucci, 2005).

The present study aims to investigate the patterns of evolution of life-history strategies and their relationship with short- and long-term plastic responses to different plant hosts by using an experimental evolution setup. An experimental evolution approach offers a unique opportunity to study evolutionary changes in real time, that is, to track genetic, physiological and developmental mechanisms that underlie the host shift process. We used laboratory populations of the seed beetle (*Acanthoscelides obtectus*), which have evolved on optimal (common beans) and suboptimal (chickpea) plant hosts for more than 35 years, as well as populations selected for high developmental plasticity on common beans and chickpeas alternating as plant hosts each generation. This insect species is a specialist that uses plant species from the same family. Specifically, the aims of this work were to determine: (1) how short- and long-term exposure to different hosts (beans and chickpeas) affect life-history traits in laboratory populations of the seed beetles; (2) whether selection for high developmental plasticity changes life-history responses to interspecific host variation compared to populations adapted to beans and chickpeas; and (3) whether there are differences in host shift potential between populations selected for host plasticity and populations adapted to the two host plants.

MATERIALS AND METHODS

Study species

The work presented in this paper was performed on the seed beetle, *Acanthoscelides obtectus* (Coleoptera: Chrysomelidae: Bruchinae). This holometabolous insect is frequently found in legume storages around the world and is specialised for plant hosts in the Fabaceae family. Since storages often resemble conditions in the laboratory (e.g., temperature, humidity levels), this species has proven to be a valuable model for long lasting, laboratory evolution experiments (Savković et al., 2016, 2019; Stojković et al., 2014; Tucić et al., 1996). The seed beetles are facultatively aphagous, and adults obtain all resources needed for somatic maintenance and reproduction while developing inside a legume seed. Development of larval phases and pupation takes around 30 days to complete. Finally, just 2 h after emergence, adults can copulate.

Rearing conditions and laboratory stock populations of the seed beetles

Rearing conditions of all laboratory populations of the seed beetles used in this experiment were constant (i.e., insect rearing chambers were without available light set at 30°C ± 0.1°C with relative humidity 30% ± 1%). Insects were reared in glass jars, and no additional food or water was offered to them during adulthood. Potentially harmful effects of inbreeding were avoided by randomly taking at least 600 individuals that contributed to the subsequent generations of each population. Overlap between generations was prevented, and individuals from different generations were not mixed. In order to evade potential contamination, food for larvae (white common bean seeds and chickpeas) was frozen for 48 h on −20°C before being used in the experiment. All seeds were pesticide free products.

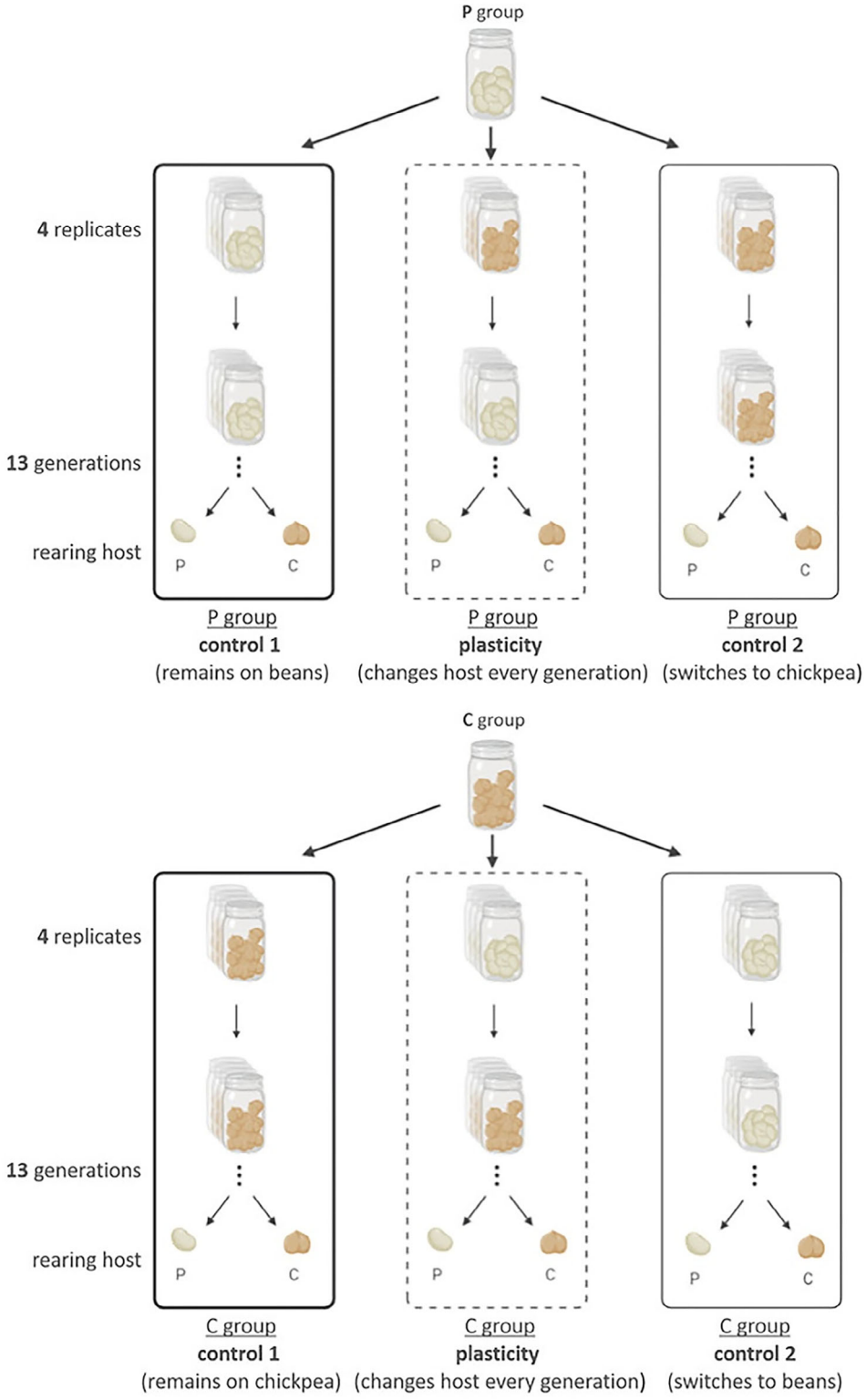

FIGURE 1 Experimental design. Two stock laboratory populations were used at the start of the experiment: One reared on common beans (P group) and the other reared on chickpeas (C group). Three treatments were established from each group: Control 1 (insects remain on the same host as the original group - bolded lines), plasticity (insects are changing the host every generation - dashed lines) and control 2 (insects are reared on a plant host different to the original group - solid lines). Each treatment group had four replicate populations that were in the experiment for 13 generations before life-history traits performance was assayed on both hosts (rearing host).

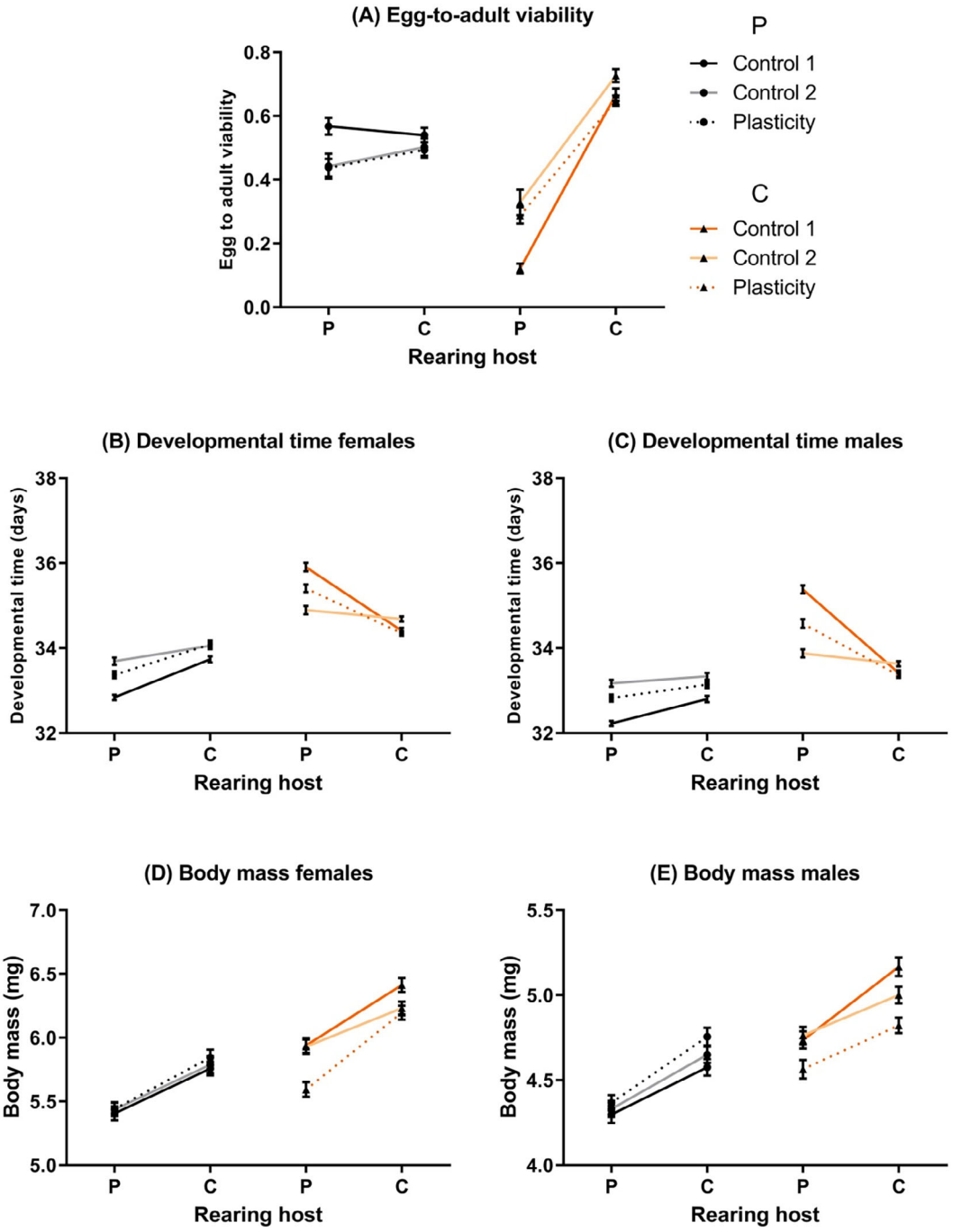

FIGURE 2 Mean values and SE of life-history traits of seed beetle individuals originated from P and C groups. Number of replicated data (N) is indicated in parenthesis. Represented in the panels are: (a) egg-to-adult viability ($N_{(p)} = 116$; $N_{(c)} = 140$); (b) developmental time females ($N_{(P)} = 3532$; $N_{(C)} = 3821$); (c) developmental time males ($N_{(P)} = 3832$; $N_{(C)} = 4004$); (d) body mass females ($N_{(P)} = 763$; $N_{(C)} = 726$); (e) body mass males ($N_{(P)} = 762$; $N_{(C)} = 726$).

Seed beetles used in this experiment have originated from stock laboratory populations maintained under constant conditions for more than 35 years. Laboratory stock populations of the seed beetles reared on common beans (251 generations, hereafter referred to as 'Phaseolus' or P group) or chickpeas (236 generations, hereafter referred to as 'Cicer' or C) were used for establishing the treatment (experimental) groups needed for this experiment (see Experimental design and procedures). Laboratory stock populations were created in 1983 from a large collection of infected bean seeds obtained from several legume storages (Tucić et al., 1996).

Experimental design and procedures

Schematic representation of the experimental design can be seen in Figure 1. Three experimental (treatment) groups were established

TABLE 1 GLMM analysis for egg-to-adult viability and mixed-model ANOVA for life-history traits: Developmental time (females and males) and body mass (females and males).

	Egg-to-adult viability	
	Wald χ^2 (d.f.)	*p*
Intercept	30.65 (1)	<0.001
Group (G)	8.67 (1)	0.003
Treatment (T)	5.38 (2)	0.068
Rearing host (R)	1970.82 (1)	<0.001
G × T	3.76 (2)	0.152
G × R	1037.86 (1)	<0.001
T × R	155.31 (2)	<0.001
G × T × R	158.53 (2)	<0.001

	Developmental time females		Developmental time males	
	F value (d.f.)	*p*	F value (d.f.)	*p*
Group (G)	62.49 (1, 18.24)	<0.001	33.81 (1, 18.18)	<0.001
Treatment (T)	0.19 (2, 18.24)	0.827	0.02 (2, 18.18)	0.985
Rearing host (R)	16.26 (1, 7353)	<0.001	98.62 (1, 7806)	<0.001
G × T	1.77 (2, 18.24)	0.199	3.05 (2, 18.18)	0.072
G × R	299.71 (1, 7353)	<0.001	283.81 (1, 7806)	<0.001
T × R	5.19 (2, 7353)	0.006	13.78 (2, 7806)	<0.001
G × T × R	28.39 (2, 7353)	<0.001	38.02 (2, 7806)	<0.001
Populations (G × T)	16.95 (18, 7353)	<0.001	23.53 (18, 7806)	<0.001

	Body mass females		Body mass males	
	F value (d.f.)	*p*	F value (d.f.)	*p*
Group (G)	56.33 (1, 18.07)	<0.001	71.85 (1, 18.11)	<0.001
Treatment (T)	1.50 (2, 18.06)	0.250	1.28 (2, 18.10)	0.342
Rearing host (R)	161.54 (1, 1459)	<0.001	122.23 (1, 1458)	<0.001
G × T	2.93 (2, 18.06)	0.079	7.61 (2, 18.10)	0.004
G × R	1.50 (1, 1459)	0.221	0.18 (1, 1458)	0.675
T × R	2.91 (2, 1459)	0.055	0.47 (2, 1458)	0.622
G × T × R	1.33 (2, 1459)	0.264	1.99 (2, 1458)	0.137
Populations (G × T)	3.36 (18, 1459)	<0.001	2.10 (18, 1458)	0.005

Note: Fixed factors in mixed-model include: Group (G), treatment (T), rearing host (R), group × treatment (G × T); group × rearing host (G × R); treatment × rearing host (T × R); group × treatment × rearing host (while random factors are represented with replicated populations nested within the group × treatment interaction). Presented are F values, degrees of freedom (d.f.) and corresponding *p* values.

from each P and C beetle populations: control 1, plasticity, and control 2. Control 1 was a treatment group in which insects continued to develop on the plant host identical to the original group, while in control 2, the plant host was the opposite of the original group. For the P group, beetles in the control 1 experimental group continued to develop on beans, while beetles in the control 2 were placed on chickpeas. Such an approach simulated the host shift process. On the other hand, for the C group, control 1 was an experimental group in which seed beetles were maintained on chickpeas, while control 2 was reared on beans. This design enabled a test of reversal host shift, that is, the situation in which beetles reared on the secondary plant host returned to their primary host. Finally, in the plasticity treatment groups, each generation of beetles alternates between common beans and chickpeas as substrates for development. In this way, it is possible to test the evolution of developmental plasticity per se and its influence on host shift potential.

Each treatment group had four replicate populations in order to exclude the effect of stochastic processes (i.e., genetic drift) on evolutionary pathways. To assess the levels and patterns of developmental plasticity in each experimental group after 13 generations (around 15 months) of selection under the described experimental setup, beetles were reared on both plant hosts for one generation (Figure 1). Life-history assays included egg-to-adult viability, developmental time, body mass, and adult (lifespan and fecundity) life-history traits. In total, 48 experimental groups were assayed (2 groups × 3 treatments × 4 populations × 2 rearing hosts).

In order to evaluate life-history traits, the following procedure was applied to all populations in the experiment. From each of the 48 experimental groups, approximately 300 randomly chosen individuals were placed into a glass Petri dish with a few seeds in order to stimulate females to lay eggs. After 24 h, laid eggs were counted and half of them were placed on around 100 bean seeds and the other half were placed on around 150 chickpeas. The procedure was repeated several times. Created replicates were placed into insect rearing chambers where they completed larval development. After approximately 32 days of development, adult beetles started to appear from seeds, and each day the number of emerged individuals was recorded, their sex was determined, and body mass was measured. Having the information about the number of eggs and emerging individuals, we calculated the egg-to-adult viability. In addition, daily records of emerged individuals enabled the assessment of developmental time for individuals of each sex. In order to measure lifespan and the number of laid eggs, randomly chosen emerging beetles were paired and observed each day. In total, 1489 beetle pairs were used in life-history assays (experimental groups ranged between 24 and 43 beetle pairs).

Statistical procedures

Binomial generalised linear mixed model (GLMM) was performed to analyse egg-to-adult viability using glmmTMB and car packages and a type III Wald chi-square test in R (version 4.2.2; R Core Team, 2022). A mixed-model ANOVA was applied for all other traits using the GLM procedure, Type III sum of squares, and Satterthwaite's approximation of denominator synthesis (SAS Institute Inc., 2010).

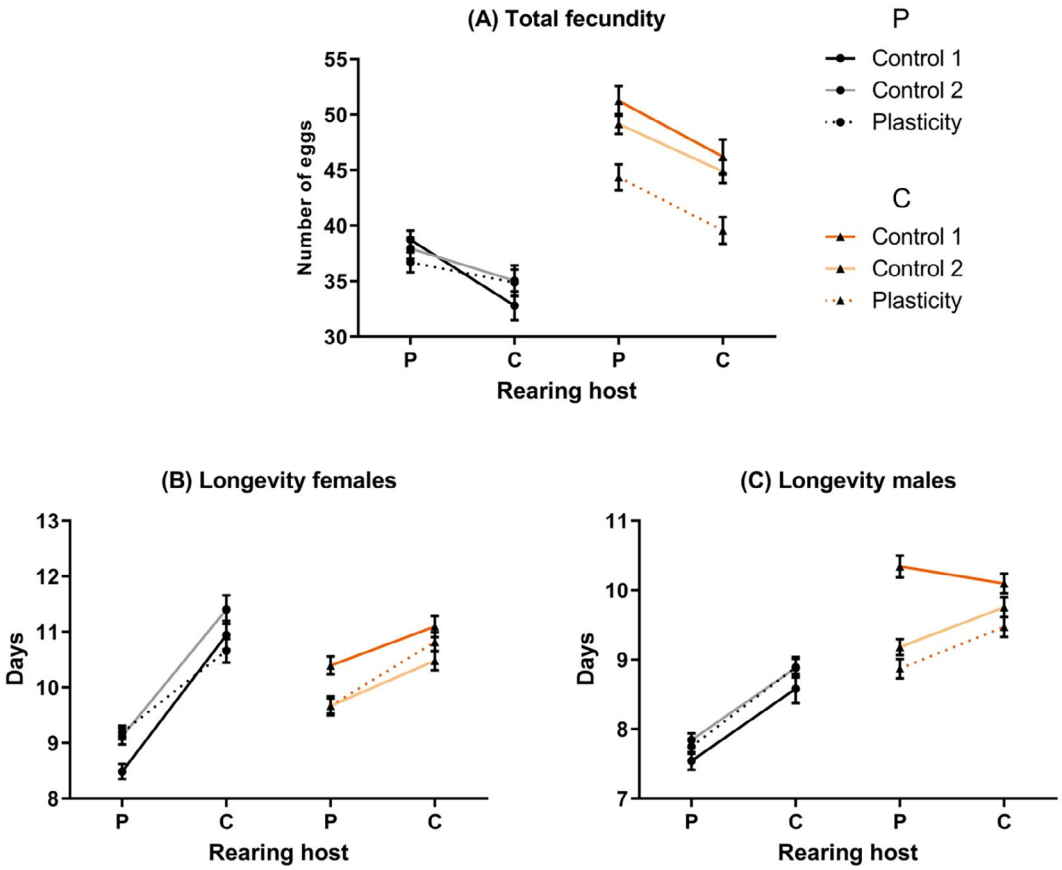

FIGURE 3 Mean values and SE of adult life-history traits of seed beetle individuals originated from P and C groups. Number of replicated data (N) is indicated in parenthesis represented in the panels are: (a) Total fecundity ($N_{(p)} = 761$; $N_{(c)} = 725$); (b) longevity females ($N_{(P)} = 751$; $N_{(C)} = 712$); (c) longevity males ($N_{(P)} = 752$; $N_{(C)} = 710$).

The full model for life-history traits included fixed (group - G, treatment - T, rearing host - R, and their interactions – group × treatment; group × rearing host; treatment × rearing host; group × treatment × rearing host) and random (replicated populations nested within the group × treatment interaction) factors. In order to improve the skewness of the data for longevity, a log transformation has been performed and used in the analysis.

RESULTS

Egg-to-adult viability, developmental time and body mass

Life-history traits demonstrated divergent patterns between bean (P) and chickpea (C) groups (Figure 2, Table 1). Differences between groups for the egg-to-adult viability were observed from the G × T × R interaction in the GLMM full model (Wald $\chi^2 = 158.53$; d.f. = 2; $p < 0.001$). Such differences were even more conspicuous when P and C groups were analysed separately. For example, out of the 116 replicates in the P group, mean values for egg-to-adult viability ranged between 0.44 ± 0.03 (Mean ± SE) and 0.57 ± 0.03, and there was no significant difference between treatments (Wald $\chi^2 = 0.69$; d.f. = 2; $p = 0.709$), while the effects of rearing the host (Wald $\chi^2 = 4.24$; d.f. = 1; $p = 0.04$) and treatment × rearing host interaction (Wald $\chi^2 = 29.11$; d.f. = 2; $p < 0.001$) were significant. It was particularly interesting to observe that individuals with the plasticity treatment within the P group had similar values across hosts. In contrast, beetles originated from the C group were very sensitive when developed on beans with low values of egg-to-adult viability ranging from 0.12 ± 0.02 to 0.32 ± 0.04 (77 replicates, highly significant effect of the rearing host, Wald $\chi^2 = 1970.99$; d.f. = 1; $p < 0.001$). Furthermore, the highest recorded egg-to-adult viability values were observed when C beetles were reared on chickpeas (from 0.65 ± 0.02 to 0.72 ± 0.02 in 63 replicates), indicating a high level of developmental specialisation for this host. In addition, significant effects of treatment (Wald $\chi^2 = 6.79$; d.f. = 2, 6.04; $p = 0.033$) and treatment × rearing host interaction (Wald $\chi^2 = 155.31$; d.f. = 2; $p < 0.001$) within the C group demonstrated response patterns that were different from the ones seen in the P group where such effects were not observed. While plasticity and control 2 treatments demonstrated similar responses after rearing on beans and chickpeas, significant effects of treatment and treatment × rearing host interaction originated from low values of egg-to-adult viability in the control 1 treatment after rearing on beans (Figure 2a).

TABLE 2 Mixed-model ANOVA for adult life-history traits: Total fecundity and longevity (females and males).

	Total fecundity	
	F value (d.f.)	***p***
Group (G)	138.81 (1, 18.34)	<0.001
Treatment (T)	6.70 (2, 18.12)	0.007
Rearing host (R)	40.01 (1, 1456)	<0.001
G × T	6.52 (2, 18.12)	0.007
G × R	0.96 (1, 1456)	0.328
T × R	1.39 (2, 1456)	0.250
G × T × R	0.43 (2, 1456)	0.653
Populations (G × T)	1.58 (18, 1456)	0.058

	Longevity females		Longevity males	
	F value (d.f.)	***p***	**F value (d.f.)**	***p***
Group (G)	4.15 (1, 18.04)	0.057	43.39 (1, 18.03)	<0.001
Treatment (T)	0.08 (2, 18.03)	0.927	0.89 (2, 18.03)	0.428
Rearing host (R)	204.20 (1, 1433)	<0.001	66.64 (1, 1432)	<0.001
G × T	2.30 (2, 18.03)	0.129	3.88 (2, 18.03)	0.040
G × R	33.38 (1, 1433)	<0.001	23.96 (1, 1432)	<0.001
T × R	0.27 (2, 1433)	0.764	4.00 (2, 1432)	0.019
G × T × R	8.49 (2, 1433)	<0.001	2.68 (2, 1432)	0.069
Populations (G × T)	6.45 (18, 1433)	<0.001	7.02 (18, 1432)	<0.001

Note: Fixed factors include: Group (G), treatment (T), rearing host (R), group × treatment (G × T); group × rearing host (G × R); treatment × rearing host (T × R); group × treatment × rearing host (while random factors are represented with replicated populations nested within the group × treatment interaction). Presented are F values, degrees of freedom (d.f.) and corresponding *p* values.

Beetles that originated from the C group had a longer egg-to-adult developmental time compared to beetles from the P group (Figure 2b,c). Such an effect was observed in both sexes (Table 1, females: F = 62,49; 1, 18,24; $p < 0.001$; males: F = 33,81; 1, 18,18; $p < 0.001$). It is worth noting that beetles from the C group developed even slower when placed on beans (significant effect of the rearing host in the by group analysis females: F = 219.32; 1, 3806; $p < 0.001$; males: F = 332.56; 1, 3989; $p < 0.001$). Prolonged development within bean seeds, together with low larval viability, reveals difficulties for the C individuals to develop on bean substrate and demonstrates a high level of developmental specialisation on chickpea.

All analysed groups demonstrated similar trends for body mass (Figure 2d,e). In general, individuals that developed on chickpeas increased their body mass, and beetles from the C group were significantly heavier than beetles from the P group (Table 1, females: F = 56.33; 1, 18.07; $p < 0.001$; males: F = 71.85; 1, 18.11; $p < 0.001$). Interestingly, despite prolonged development, values of body mass in the C group were not increased when developed on beans. Furthermore, the plasticity treatment within the C group had decreased values of body mass regardless of the rearing host compared to other treatments.

Adult life-history traits

Analysed adult life-history traits included total fecundity and longevity in both sexes (Figure 3, Table 2). Investment in reproduction, quantified as a total number of deposited eggs over a lifetime, was significantly higher in the C group when compared to the P group (F = 138.81; 1, 18.34; $p < 0.001$). This increase was even more conspicuous when females from the C group were reared on beans (highly significant effect of rearing host in the by group analysis, F = 24.08; 1, 710; $p < 0.001$). On the other hand, when females from the P group were reared on chickpeas, mean egg laying activity was reduced (e.g., from 38.74 ± 0.81 on beans to 32.79 ± 1.29 on chickpeas in the control 1 group; $n = 121$ in both groups). The plasticity treatment from the C group had lower values of total fecundity compared to control 1 and control 2, although it was still higher than any treatment from the P group. Observed differences in total fecundity were reflected in the prolonged lifespan of females with reduced fecundity (e.g., the P group reared on chickpeas). Interestingly, a similar trend was recorded in male longevity.

DISCUSSION

The process of host shift is a significant challenge for insect populations. After initial, primary contact of adults with a new plant host, phytophagous insects first need to invest their reproductive efforts in this new context. Thus, at the beginning, the host shift elicits behavioural modifications that influence oviposition preferences of females via various chemical cues of a plant host (Anderson & Anton, 2014; Katte et al., 2022; Storeck et al., 2000). The next phase during the process of host shift presumes successful development (from an egg to adult) on a new plant host. As was shown in numerous studies, shifting the plant host alters developmental trajectories of insects and causes physiological changes that might help insects to digest new food sources (Ali & Agrawal, 2012; Janković-Tomanić et al., 2015; Kergoat et al., 2005, 2005). Ultimately, if external cues (i.e., novel plant host) continue to persist through generations, transgenerational exposure to a novel host represents a selective pressure that can alter life-history strategies and consequently influence population dynamics (Tanga et al., 2013).

This study applied laboratory evolution experimental setup and examined the potential of the seed beetle to plastically respond to switching of plant hosts and to evolve developmental plasticity. Presented results demonstrated significant divergence in both life-history traits and their plasticity between the P and C experimental groups. Generally, the beetles adapted to chickpeas are larger, live longer, and lay more eggs than beetles evolved on common beans (Savković et al., 2016). In other words, evolution on the novel host for 35 years, resulted in a novel life-history strategy for the seed beetle. Other examples of long-term laboratory evolution on different hosts are also well known in *Callosobruchus maculatus*, where a response to selection was demonstrated for many different traits including lifetime fecundity, longevity, development time, and host

acceptance (Fox et al., 2009; Gompert & Messina, 2016; Messina et al., 2009; Messina et al., 2020).

Our experiments on *A. obtectus* showed that experimental populations also diverged regarding the patterns of plastic responses to alternative plant hosts, indicating different strategies for overcoming physiological and developmental stress when shifted to novel plant seeds. Common bean and chickpea seeds have distinct chemical and physical characteristics. It is known that insecticidal proteins and secondary metabolites, their concentrations, and structure differ between chickpea and bean seeds (see references in Janković-Tomanić et al., 2015). The beetles originating from populations maintained on optimal hosts (i.e., common beans) had equally successful larval survival as those developed within chickpeas. It is likely that the P females produce high quality eggs and embryos with sufficiently plastic physiological mechanisms that contribute to the stable viability across different plant hosts. In contrast, in populations adapted to chickpea, high mortality of embryos and larvae within common bean seeds, as well as significantly prolonged pre-adult development on this substrate, suggest low levels of adaptability (i.e., plasticity) in the underlying physiology of the variable chemical composition and physical features of seeds. Therefore, it could be concluded that the seed beetles evolved high levels of specialisation on a once suboptimal plant host. However, in their adulthood, beetles from the two selection regimes show a completely opposite trend in their ability to maintain on the alternative hosts. Generally, P beetles invest less in their reproductive output and drop their fecundity even more when faced with chickpea seeds, whereas chickpea-adapted individuals further increase the number of eggs laid on bean seeds compared to egg-number on chickpeas. Observed responses in reproductive behaviour are in line with previous work conducted on *A. obtectus* populations that evolved on chickpea. These studies have demonstrated decreased capacity to discriminate between seeds for oviposition (Savković et al., 2016) and also decreased choosiness for sexual partners (Stojković et al., 2014) indicating disruptions in the sensory collection/processing capabilities of the C beetles (Carrasco et al., 2015). Recent studies in *C. maculatus* have also demonstrated that short term changes can affect gene expression patterns (e.g., cytochrome P450s and beta-glucosidase) that play particularly important roles in the process of adaptation to a new host (Rêgo et al., 2020). Furthermore, some other examples from seed beetles have shown that increased sexual selection can affect the rate of adaptation to the novel host and result in the host-specific reinforced effects of natural and sexual selection (Fricke & Arnqvist, 2007).

Generally, it seems that a low pre-adult survival in chickpea-adapted *A. obtectus*, when developed on bean seeds, is compensated with high fecundity in the adult period. This apparent pre-adult/adult asymmetry in response of life-history traits has been repeatedly demonstrated in these experimental populations (Savković et al., 2016; Tucić et al., 1997) and clearly shows that plasticity is important for initial population survival. In addition, observed short-term responses resemble long-term changes detected in populations adapted to chickpea, indicating that plasticity could determine the evolutionary pathways of shifted populations (Stojković et al., 2014). Knowing that diverse life-history traits are an integrative aspect of organisms' fitness (Fox & Messina, 2018), their variability can lead to the evolution of different life-history strategies and to the evolution of different ways to maintain stable populations across environments.

The aspect of time in the process of evolution was clearly demonstrated in our experiment through the results obtained on control 2 and plasticity treatments. These treatments were created from the samples of beetles that originated from the stock laboratory populations maintained on either common beans or chickpea for more than 35 years and had evolved for only 13 generations (around 15 months) prior to the experiments. Given that the beetles were placed on the alternative hosts, the control 2 treatment represents the novel host shift from the optimal (common beans) to the suboptimal (chickpea) plant host and the reverse host shift from chickpea to common beans. Results obtained on the plasticity treatments reveal the potential of the developmental plasticity to evolve during 13 generations. Being that the seeds of the two species have different physical and chemical characteristics, it could be expected that these changing conditions in subsequent generations impose strong physiological challenges and a need for frequent changes of larval developmental trajectories, that is, high plasticity of underlying processes. It has been clearly shown that 13 generations of host shift on chickpeas were not enough to reach the same level of specialisation in the pre-adult period as seen in populations that were reared on chickpeas for many generations. Furthermore, the plasticity treatment originated from the P group and has not shown differences in plasticity patterns compared to the controls. Demonstrated high potential of P beetles to respond well to alternative environments through pre-adult development suggests that the evolution of plasticity could be limited because further increase in plasticity levels can be costly and not likely to evolve in a few generations (DeWitt et al., 1998; Snell-Rood et al., 2018). Patterns of the life-history plasticity in the plasticity treatment also remained unchanged compared to controls within the C experimental group. The reverse host shift again showed the low ability of individuals from the C group to adjust their pre-adult development on different hosts. It is probable that the amount of genetic variability of developmental plasticity of the pre-adult period was too low for the evolution of novel patterns of adaptive plastic responses to once optimal plant host, at least for the given time. The constantly demonstrated drop in survival of C beetles on bean seeds, even in populations selected for developmental plasticity, indicates extreme specialisation of development in chickpea. In other words, it could be hypothesised that strong selection on early developmental stages, after the shift to a suboptimal host, purged underlying genetic variation and limited the evolution of pre-adult traits and their plasticity. The potential for the evolution of plasticity has been observed only for some life-history traits, given that fecundity, lifespan and body mass in plasticity treatments from the C group converged towards values assessed in P beetles.

According to the oscillation hypothesis, a generalist species would specialise on a certain plant host and exploit the benefits of a narrow ecological niche (Janz & Nylin, 2008; Nylin et al., 2014). If conditions are favourable, however, a specialised species could evolve in the

direction of a generalist. Results obtained in this study demonstrate the potential of *A. obtectus* to evolve from generalist towards specialist, but not in the opposite direction, at least in a short amount of time. We hypothesize that a specialist could evolve in a generalist direction for adult life history traits, but less likely for pre-adult life history traits. Perhaps, over a longer period of time, with the accumulation of novel genetic variation, novel pathways for adjusting physiological responses to bean seeds could evolve. Our experiment on a reverse host shift showed that evolutionary modelling of life-history strategies in insects could pass through different stages and could be managed by patterns of developmental plasticity.

AUTHOR CONTRIBUTIONS

Uroš Savković and Biljana Stojković designed the experiment; Uroš Savković, Lea Vlajnić, Mirko Đorđević and Sanja Budečević conducted the experiments; Uroš Savković analysed the data; Uroš Savković wrote the initial version of the manuscript; Uroš Savković, Mirko Đorđević, Lea Vlajnić, Sanja Budečević and Biljana Stojković contributed to the revision process equally.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1.

Table S2.

Table S3.

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