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Within-generational but not cross-generational effects of host plant on *Myzus persicae* performance and preferences

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Abstract

Myzus persicae (Sulzer) (Hemiptera:Aphididae) aphids feed on a wide range of host plants but exhibit strong preferences for plants from some families, particularly Brassicaceae. Previous studies demonstrate local adaptation of *M. persicae* populations, where populations collected on a given host plant have increased performance on this host, highlighting the potential for plant preferences and fitness to shift through cross-generational changes or rearing on different plants within generations. Endosymbionts living within aphid cells can have substantial impacts on aphid fitness and also influence host plant responses. *Rickettsiella* is a facultative endosymbiont that shows potential biocontrol applications due to its host fitness costs, but it is unclear if costs change when aphids are reared on different host plants across generations. In experiments with two *M. persicae* lines (one carrying a transinfection of *Rickettsiella*) we show that maintenance for 15 generations on leaf discs of three different host plants (bok choy, clover and potato) had little effect on fitness when reciprocally tested on each host plant. Fitness was mainly influenced by the host plant used for testing compared with cross-generational effects. In two-choice Petri dish experiments involving bok choy and clover, maintenance for 15 generations on either plant had no effect on plant preferences, but aphids acclimated to clover shifted their preference towards clover. The transinfected endosymbiont *Rickettsiella* was stable in all lines, where its deleterious effects and body colour alterations were not dramatically modified by the host plant used for maintenance or testing. This study highlights the adaptability of *M. persicae* to diverse host plants, stable transinfected endosymbiont effects and the importance of within-generational host plant effects for fitness, with implications for the use of endosymbionts for pest management.

KEYWORDS
biocontrol, clonal lines, facultative endosymbiont, fitness cost, green peach aphid, host acclimation, host preference, pest management, *Rickettsiella*, two-choice experiment

INTRODUCTION

Aphids are globally important pests of agricultural crops due to damage caused by phloem feeding and the transmission of plant pathogens. *Myzus persicae* (Sulzer) (Hemiptera:Aphididae) is the most important aphid virus vector in the world due to its widespread distribution, polyphagous nature and competence as a vector of many important pathogens, including turnip yellows virus (CABI, 2022). As a generalist, *M. persicae* can also be a problem for household plants and horticultural crops but exhibits preferences for plants from some families, including the economically important Brassicaceae and Solanaceae (CABI, 2022). The control of this species is particularly challenging due to its high reproductive capacity and its rapid evolution of resistance to chemical insecticides (Bass et al., 2014; Troczka et al., 2021; Ward et al., 2024). Furthermore, many insecticides with efficacy against *M. persicae* have been withdrawn from the market or banned in some jurisdictions (Dewar & Qi, 2021; Hillocks, 2013).

The performance of, and problems caused by, *M. persicae* can differ considerably across host plants (Altesor & González, 2023; Hong et al., 2019) and even between cultivars of a single species (Goundoudaki et al., 2003; La Rossa et al., 2013). There is also intraspecific variation in host plant performance and preferences across its range, where some genotypes perform better or prefer some plant hosts over others (Lowe, 1973; Nikolakakis et al., 2003; Troncoso et al., 2005). This is supported by genetic studies that have identified associations between genotype and the host plant on which aphids were collected (Margaritopoulos et al., 2007; Singh et al., 2021; Weber, 1985). Evidence for local adaptation of *M. persicae* to host plants is demonstrated by the emergence of the *M. persicae nicotianae* subspecies, which shows an increased preference for tobacco (Margaritopoulos et al., 2005), increased fecundity on tobacco (Ramsey et al., 2014) and resistance to nicotine produced by this plant (Bass et al., 2013).

Variation in the performance of aphids on different host plants highlights the potential for aphid populations to adapt to host plants through cross-generational changes or through host acclimation triggered by plant exposure. Acclimation can be defined as a physiological adjustment by an organism in response to environmental change, which represents a form of plasticity that can be separated from cross-generational plasticity or fixed genetic changes (Hoffmann & Bridle, 2022). Past studies have highlighted cross-generational effects of host plant on performance which can depend on the aphid clone tested (Lowe, 1973; Olivares-Donoso et al., 2007). While some studies show that prior rearing on host plants can increase performance on that plant in the subsequent generation (e.g. Ramsey et al., 2014), relatively few studies have separated the effects of acclimation within a generation from cross-generational effects through host plant switching experiments. Li et al. (2015) found that populations of *M. persicae* maintained on tobacco or rape for 10 generations and reciprocally tested on both host plants generally had higher fitness on the plant used for maintenance, but patterns were temperature dependent. Host plant preferences as well as aphid performance on the host can also be influenced by cross-generational effects (McLean et al., 2009; Via, 1991) and shift with acclimation (Gorur et al., 2007) although patterns for preferences and performance do not necessarily match (Altesor & González, 2023).

All aphids carry obligate endosymbionts, which are deemed essential for aphid reproduction (Moran, 2021) and frequently carry facultative endosymbionts (Henry et al., 2015; Zytynska & Weisser, 2016) which induce a broad spectrum of phenotypic effects. Facultative endosymbionts generally induce host fitness costs under benign conditions while providing conditional benefits, particularly resistance to mummification from parasitoid attacks (Vorburger & Gouskov, 2011; Zytynska et al., 2021). Facultative endosymbionts often influence relative performance on different host plants (Chen et al., 2000) and the frequencies and composition of endosymbionts found within aphids can vary between host plants in nature (Brady & White, 2013; Vorburger et al., 2017; Xu et al., 2020). The presence of *Arsenophonus* (Wagner et al., 2015) and *Regiella* (Mahieu et al., 2024; Ramírez-Cáceres et al., 2019; Tsuchida et al., 2004) endosymbionts has been linked to host plant specialization in some aphids, where the endosymbionts can greatly enhance performance on one host plant at the cost of performance on another. While *Arsenophonus* is absent from *M. persicae* (Yang, Umina, et al., 2023), *Regiella* occurs naturally at a low frequency (Vorburger et al., 2010) but any association with host plant species is unknown.

The manipulation of endosymbionts is a potential avenue for biological pest control in aphids and other pest insects (Douglas, 2007; Zindel et al., 2011). For instance, by transferring facultative endosymbionts between species, novel traits can be introduced to aphids which may benefit growers, such as a reduction in plant virus transmission (Gong et al., 2020) or reduced fitness of the insect host (McMeniman et al., 2009) which may decrease feeding damage and population growth. Facultative endosymbionts can only be used for such approaches if there is a mechanism that allows them to spread through and persist in field or greenhouse populations. For aphids which are mainly parthenogenic, plant-mediated horizontal transmission has been observed for several facultative endosymbionts (Chrostek et al., 2017) and is one route by which they could spread through aphid populations (Gu et al., 2023; Li et al., 2018).

The facultative endosymbiont *Rickettsiella viridis* (hereafter denoted *Rickettsiella*) is one candidate for biological control applications due to high frequencies of horizontal transmission coupled with strong host fitness costs in some aphid hosts (Gu et al., 2023). Although *Rickettsiella* is uncommon in natural aphid populations and not present in *M. persicae* naturally (Yang, Gill, et al., 2023; Yang, Umina, et al., 2023), it can be readily transferred between species through microinjection (Gu et al., 2024). In *M. persicae*, the endosymbiont also modifies body colour, and this can be used as a phenotypic marker (Gu et al., 2023) as well as being potentially important in relation to protection against predation, as shown for *Rickettsiella* in pea aphids (*Acyrthosiphon pisum*) Harris (Polin et al., 2015). Models suggest that the release of *M. persicae* with transinfected *Rickettsiella* could suppress aphid populations in some climates if the frequency of horizontal transmission is sufficiently high (Slavenko et al., 2024). However, this relies on *Rickettsiella* exerting stable effects under a range of environments, including different host plants. We previously evaluated the effects of *Rickettsiella* in *M. persicae* on a range of host plants and found consistent, high frequencies of horizontal transmission but some differences in fitness costs across host plants (Ross et al., 2024). There are currently no studies testing whether fitness costs of facultative endosymbionts in aphids can change during maintenance on different plants. Given that endosymbionts including *Rickettsiella* can be involved in nutritional provisioning but also compete for host resources (Caragata et al., 2014; Floriano et al., 2024; Price et al., 2021), this may lead to differential performance on host plants across generations.

In this study, we performed experiments with *M. persicae* with or without the facultative endosymbiont *Rickettsiella* to test whether performance and preferences can shift with maintenance and testing on three different host plants (*Brassica rapa* subsp. *Chinensis* (Hanelt), *Trifolium repens* L and *Solanum tuberosum* L). These host plants were chosen because they represent three agriculturally important plant families (Brassicaceae, Fabaceae and Solanaceae, respectively) and also because we found differential fitness costs of *Rickettsiella* across generations on these hosts in previous experiments (Ross et al., 2024). The mechanism for this host effect was unclear; apart from causing deleterious fitness effects and changes in body colour and perhaps providing nutrition, *Rickettsiella* has so far only been associated with decreased fungal sporulation (Lukasik et al., 2013). While *M. persicae* performs well on all three hosts, it differs substantially in its nutritional content, chemical defences and presence of physical defences including trichomes (Chowański et al., 2016; Fürstenberg-Hägg et al., 2013; Levin, 1976). Our experiments were designed to separate within-generational effects of host plant from cross-generational effects through maintenance on different host plants for 15 generations followed by reciprocal testing on each plant. Any cross-generational effects are likely to reflect maternal effects or epigenetic changes rather than genetic changes due to the clonal reproduction of aphids.

METHODS

Aphid lines and laboratory culture

The *Rickettsiella* (+) and *Rickettsiella* (−) clonal lines of *M. persicae* were generated and reared as described elsewhere (Gu et al., 2023). Prior to maintenance and experiments, both lines were reared on bok choy (*Brassica rapa* subsp. *Chinensis*, var. baby bok) leaf discs (35 mm diameter) on 60 mm diameter Petri dishes containing a layer of 1% agar. Aphid lines were maintained at 10°C under an 18:6 light: dark cycle in incubators (PG50 Plant Growth Chambers, Labec Laboratory Equipment, Marrickville, NSW, Australia). Lines were tested for their endosymbiont status using qPCR assays as described previously (Gu et al., 2023). Prior to the experiments reported here, lines had been maintained in the laboratory on bok choy leaf discs for at least 50 generations at population sizes of 10–20 individuals per generation.

Maintenance on different host plants

For maintenance and experiments, all lines were maintained at 19°C under an 18:6 light: dark cycle in controlled temperature rooms. Nymphs (<24 h old) from the *Rickettsiella* (+) and *Rickettsiella* (−) lines were collected and placed on 35 mm Petri dishes with leaf discs 25 mm from either bok choy (*Brassica rapa* subsp. *Chinensis*, var. baby bok), white clover (*Trifolium repens*, var. unknown) or potato (*Solanum tuberosum* var. Désirée), with all plants being 1.5–3 months old. We established three replicate lineages per aphid line and host plant for a total of 18 lineages. Aphids were maintained in discrete generations at a population size of 10 individuals per lineage by rearing aphids to adulthood until all lines had started to produce offspring, then transferring 10 nymphs (<48 h old) at random to fresh Petri dishes. Leaf discs were replaced twice per week to maintain high quality of the plant material. These lineages were reared for 15 generations (~6 months) prior to experiments.

Life history traits and experimental design

We measured life history traits (survival to adulthood, wing formation, total nymphs produced and longevity) as an estimate of total fitness by rearing groups of aphids in Petri dishes. Thirty nymphs (<48 h old) from each of the 18 lineages (3 host plants × 2 aphid lines × 3 replicate lineages) were split into a further three Petri dishes (diameter 60 mm) per lineage with 10 nymphs each on leaf discs (diameter 35 mm) from the same host plant used for maintenance. Nymphs were reared until 10–11 day old, and then, apterous adults were placed on fresh Petri dishes to collect nymphs <24 h old for experiments.

The experimental design involved nymphs from each of the 18 lineages placed on leaf discs (diameter 25 mm) from each of the three host plants used for maintenance—bok choy, white clover or potato—ensuring that the lines were tested in all reciprocal combinations of host plant (Figure 1). We set up four Petri dishes with five aphids each per replicate lineage, for a total of 12 replicates per treatment (e.g. the treatment involving *Rickettsiella* (+) aphids maintained on potato and tested on clover). Aphids were transferred to fresh leaf material and Petri dishes twice per week to minimize effects associated with plant degradation.

Petri dishes were monitored daily where we scored the number of aphids reaching adulthood, the number of adults that became alates (winged), the number of nymphs produced and the number of adult aphids alive. We then computed the proportion of adults becoming alates by dividing the number of alates by the number of aphids that reached adulthood in each Petri dish. Average fecundity was calculated by dividing the total number of nymphs produced by the number of aphids reaching adulthood in each Petri dish. Average

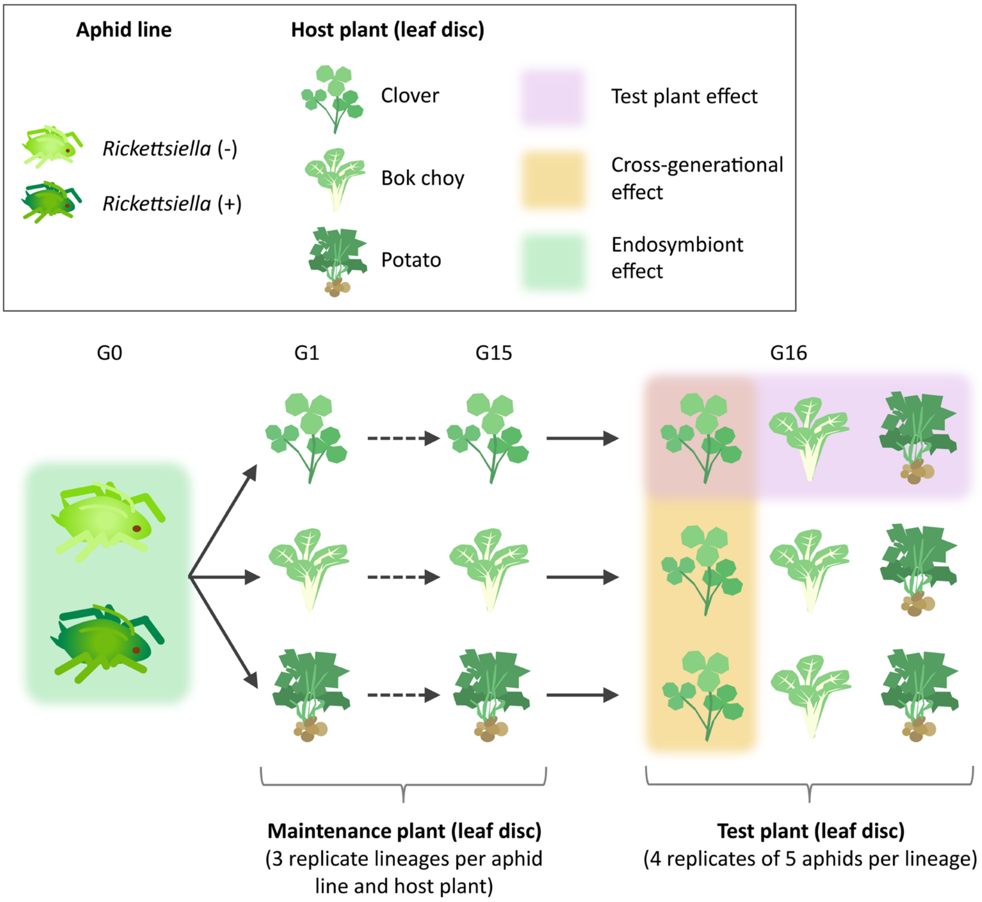

FIGURE 1 Experimental design. *Rickettsiella* (–) or (+) aphids were maintained in Petri dishes with clover, bok choy or potato leaf discs for 15 generations. We set up three replicate lineages per combination of aphid line and maintenance plant. Aphids from each treatment were then tested on each of the three host plants, allowing for tests of *Rickettsiella* effects, test plant effects (through comparisons between test plants on the same maintenance plant), cross-generational effects (through comparisons between maintenance plants on the same test plant) and their interactions. Figure shadings represent effects tested for one plant type (clover) as an example.

longevity was calculated by taking the mean survival time of aphids that reached adulthood in each Petri dish. Therefore, nymphs that died before reaching adulthood were excluded from the winged proportion, fecundity and longevity estimates. We also measured total productivity by computing the total number of offspring of each Petri dish divided by 5 (the number of initial aphids), excluding Petri dishes where no aphids survived.

We then measured the body length and body colour of individual apterous adults reared under each treatment. Body length was measured as a proxy for body size and is expected to be influenced by host plant, while body colour is a key trait modified by the presence of *Rickettsiella* (Gu et al., 2023). Fourteen-day-old aphids from the above experiment were temporarily removed from their Petri dishes and photographed individually on a white background under a dissection microscope with consistent lighting conditions according to methods described previously (Gu et al., 2023), then returned to their original Petri dish. We then measured body length and body colour separated into three components (hue, lightness and saturation) using ImageJ v.1.48 (Schneider et al., 2012) and the RGB Measure plugin (https://imagej.nih.gov/ij/plugins/rgb-measure.html). At least 20 and up to 40 aphids were measured per treatment across all replicate lineages. Alate aphids and those that had died prior to photography were excluded from the analysis.

Host plant preference

We tested the effect of the plant host used for long-term maintenance and developmental acclimation on host plant preferences between bok choy (a preferred host) and clover (a non-preferred host). Aphids from the *Rickettsiella* (+) and (–) lines maintained on bok choy or clover (pooled across all replicate lineages) were reared to adulthood on their respective host plant. We then collected nymphs (<24 h old) from each line and reared them for 4–5 day on each of the two host plants. These reciprocal transfers across generations allowed us to partially separate the effects of the long-term rearing on specific host plants and acclimation. To measure host plant preferences, we set up 60 mm Petri dishes containing a single 25 mm leaf disc each of clover (excised from one of three leaflets) and bok choy, placed side by side. We then introduced 10–15 aphids (4–5 day old) from each line onto paper towel which was placed on the underside of the Petri lid. Petri dishes were closed and inverted so that the aphids had to climb to reach the leaf discs. To reduce potential confounding effects of external environmental factors, such as lighting and host plant cues, Petri dishes from all treatments were placed in a black tub directly under plant growth lights and away from other host plants and randomized in their position. After 24 h, Petri dishes were opened and we counted the number of aphids on each leaf disc. Counts were converted to proportions of aphids that were found on the bok choy leaf disc. Aphids resting on the agar or paper towel, and those that died were excluded from the calculation. We set up 10 Petri dishes for each combination of aphid line (*Rickettsiella* (+) or (−)), maintenance plant (bok choy or clover) and acclimation plant (bok choy or clover).

Experimental design and analysis

All analyses were performed in IBM SPSS Statistics 29 for Windows. We were interested in testing the effect of maintenance plant type and test plant types with two aphid lines and three replicate lineages nested within maintenance plant type. The interactions of particular interest are maintenance × test plant as well as interactions with aphid line which may reflect different responses of *Rickettsiella* to the maintenance and test plants. For the life history traits, there were a few Petri dishes (<2%) where no offspring were produced; given that these Petri dishes may fail to produce offspring for reasons unconnected to host and infection status, we excluded these from the final analyses. Assuming a linear model for a trait, we therefore considered the design given by.

$$Y_{ijklm} = a + b_i + c_j + d_k + f_{l(i)} + e_{m(ijkl)},$$

where a is the grand mean, b_i reflects ith maintenance plant, c_j reflects the jth test plant, d_k reflects the kth (infected or uninfected) aphid line, the abovementioned interactions e_{ij}, f_{ik}, g_{jk} are included along with nested replicate lineage ($f_{l(i)}$), and interactions involving the nested factor are pooled with the overall error term as $e_{m(ijkl)}$. For the size and colour traits which were normally distributed (revealed from Shapiro–Wilk tests), we used general linear models to test for effects of aphid line, test plant, maintenance plant and their interactions. For proportional data (survival to adulthood, alate production and host plant preferences), we ran generalized linear models with a logit link function and binomial probability distributions. Since we were mainly interested in overall effects and their interactions rather than pair-wise comparisons between treatments, we did not perform post-hoc tests. In all analyses, p values <0.05 were considered to be significant.

RESULTS

Effects of host plant and *Rickettsiella* on body colour

The *Rickettsiella* (+) and (−) lines maintained on bok choy, clover and potato for 15 generations were reared reciprocally on each host plant and measured for various traits. Aphids were measured for their body colour to test whether the effects of *Rickettsiella* on this trait remained stable following maintenance on different host plants. Across all treatments, the *Rickettsiella* (+) lines were consistently darker and less saturated than their *Rickettsiella* (−) counterparts (Figure 2), with aphid line having substantial effects on the three colour components (general linear model, hue: $F_{1,534} = 88.709$, $p < 0.001$, lightness: $F_{1,534} = 529.764$, $p < 0.001$, saturation: $F_{1,534} = 323.807$, $p < 0.001$). The host plant that aphids were tested on also had a substantial impact on colour (hue: $F_{2,534} = 225.585$, $p < 0.001$, lightness: $F_{2,534} = 551.972$, $p < 0.001$, saturation: $F_{2,534} = 112.054$, $p < 0.001$). While the maintenance plant (one which aphids were maintained from G1 to G15) also significantly influenced some colour components (hue: $F_{2,6.912} = 3.155$, $p = 0.11$, lightness: $F_{2,8.672} = 54.882$, $p < 0.001$, saturation: $F_{2,6.282} = 4.241$, $p = 0.07$), these effects were weaker than those of the test plant and aphid line. This was also the case for many two-way interactions between aphid line, maintenance plant and test plant (Tables S1–S3). Replicate lineage (nested within maintenance plant) had a marginally significant effect on saturation ($F_{6,534} = 2.397$, $p = 0.03$) but not on any other trait in the experiments (Tables S1–S9).

Impacts of host plant on aphid survival, development and fecundity

We found substantial impacts of the host plant used for maintenance and testing on the survival and development of aphids. The proportion of aphids reaching adulthood was significantly influenced by the maintenance plant (generalized linear model: Wald $\chi^2 = 20.199$, df = 2, $p < 0.001$) as well as the test plant (Wald $\chi^2 = 82.725$, df = 2, $p < 0.001$), with aphids reared on clover having lower overall survival (Figure 3A,B). We also found an interaction between maintenance plant and test plant (Wald $\chi^2 = 13.576$, df = 4, $p = 0.01$), where aphids maintained on bok choy or potato and then tested on clover had particularly low survival (Figure 3A,B). There was no significant effect of aphid line (Wald $\chi^2 = 0.449$, df = 1, $p = 0.50$)

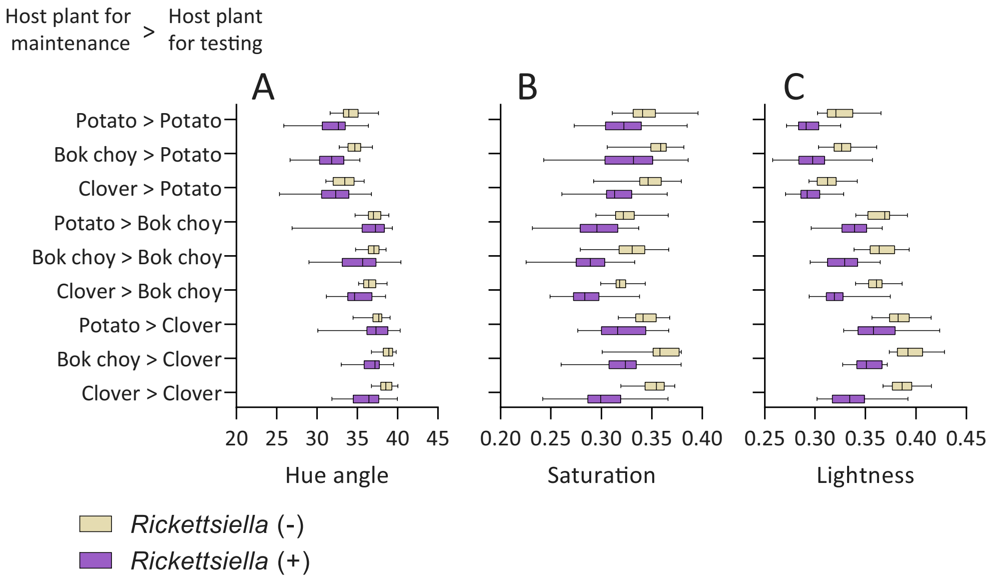

FIGURE 2 Effects of host plant and *Rickettsiella* on the body colour of *Myzus persicae* reared in Petri dishes. Body colour was separated into three components: Hue (A), saturation (B) and lightness (C). Aphids from the *Rickettsiella* (–) and (+) lines were maintained in Petri dishes on leaf discs from different host plants and then tested on new host plants or the same host plants. The boxplots show the median value and the first and third quartiles (upper and lower boxes). The whiskers show the interquartile range.

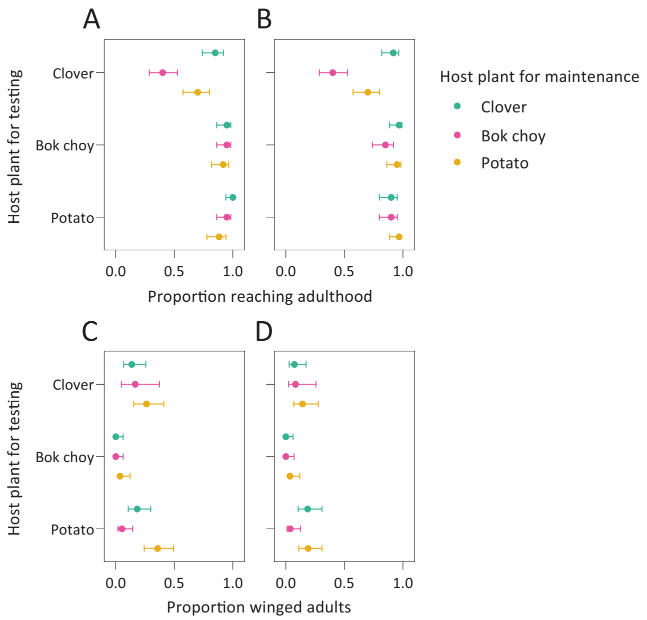

FIGURE 3 Effects of host plant and *Rickettsiella* on the proportion of *Myzus persicae* reaching adulthood (A, B) and developing wings (C, D). Aphids from the *Rickettsiella* (–) (A, C) and *Rickettsiella* (+) (B, D) lines were maintained in Petri dishes on leaf discs from different host plants and then tested on new host plants or the same host plants. Dots show the proportion of individuals reaching adulthood or developing wings based on five individuals per Petri dish with 12 replicates, and the error bars represent 95% binomial confidence intervals. Aphids that died before reaching adulthood were excluded from calculations of winged adult proportions.

or any significant two-way interactions involving aphid line (Table S4), suggesting that *Rickettsiella* infection did not affect this trait.

Host plant also influenced wing formation, with effects of both maintenance plant (generalized linear model: Wald $\chi^2 = 1728.697$, df = 2, $p < 0.001$) and test plant (Wald $\chi^2 = 1432.644$, df = 2, $p < 0.001$) on the proportion of adults with wings (alates) (Figure 3C,D). Wing formation was generally lower in aphids maintained or tested on bok choy compared with the other two host plants. We found no significant effect of aphid line on the proportion of adults developing wings or any two-way interactions (Table S5).

Aphids reaching adulthood from the different host plant treatments were measured for their fecundity, longevity, body length and total productivity (Figure 4). Here, we found substantial negative effects of *Rickettsiella* infection on fecundity (General linear model: $F_{1,192} = 160.439$, $p < 0.001$), longevity ($F_{1,192} = 238.953$, $p < 0.001$) and total productivity ($F_{1,192} = 134.005$, $p < 0.001$), despite *Rickettsiella* (+) aphids being significantly larger overall ($F_{1,530} = 37.734$, $p < 0.001$). We found no significant effect of maintenance plant for any trait (fecundity: $F_{2,6.064} = 1.246$, $p = 0.35$, longevity: $F_{2,6.155} = 0.757$, $p = 0.51$, body length: $F_{2,6.480} = 0.257$, $p = 0.78$) except for total productivity ($F_{2,6.043} = 16.561$, $p = 0.01$). This was likely influenced by reduced proportions of aphids reaching adulthood in some treatments (Figure 3A,B). In contrast to the maintenance plant, the test plant clearly influenced fecundity, longevity, body length and total productivity (Tables S6–S9), with poorer performance on potato compared with the other two host plants (Figure 4). Effects of both maintenance plant and test plant on these traits may have been influenced by differences in wing formation (Figure 3C,D). While there were relatively few significant two-way interactions between

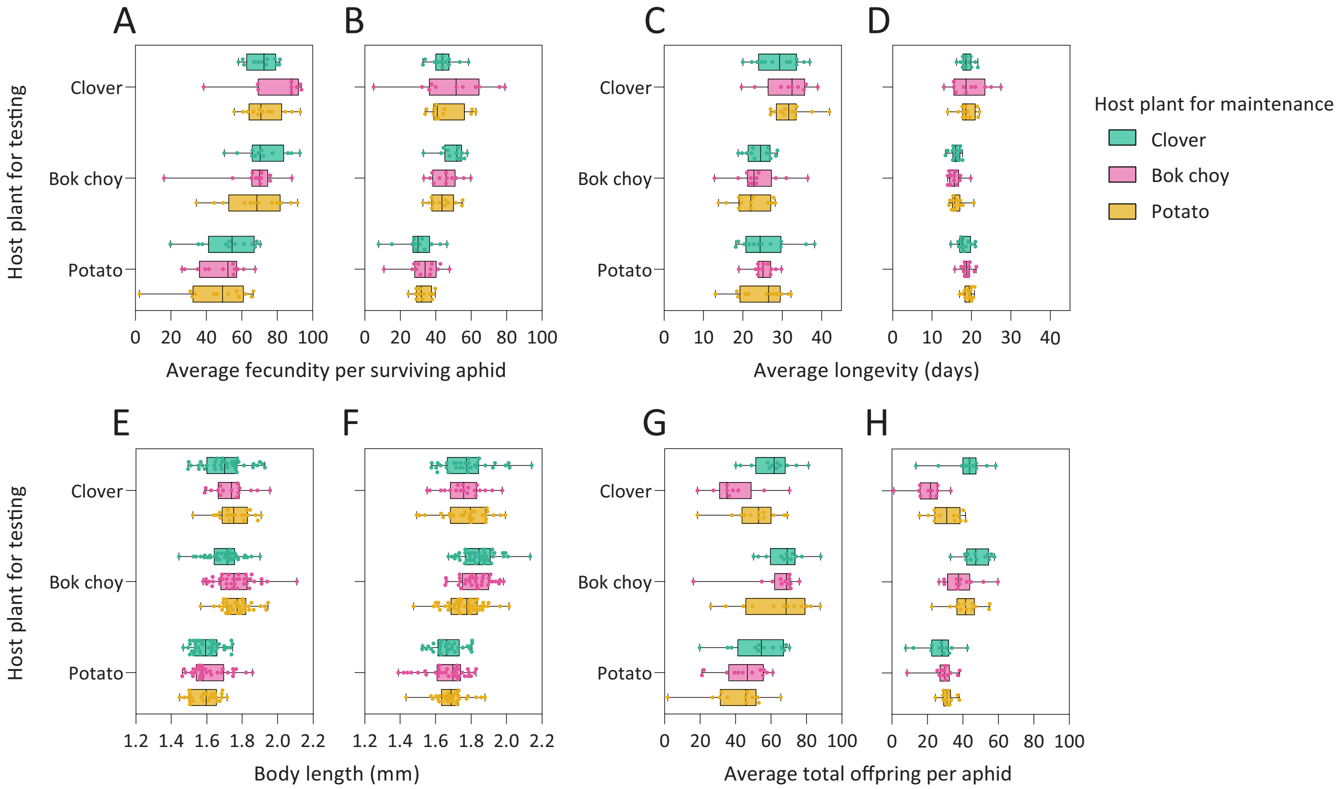

FIGURE 4 Effects of host plant and *Rickettsiella* on average fecundity (A, B), longevity (C, D), body length (E, F) and total productivity (G, H). Aphids from the *Rickettsiella* (–) (A, C, E, G) and *Rickettsiella* (+) (B, D, F, H) lines were maintained in Petri dishes on leaf discs from different host plants and then tested on new host plants or the same host plants. Fecundity represents the total number of offspring per Petri dish divided by the number of aphids that reached adulthood while average total offspring values were not adjusted for aphid mortality during development. The boxplots show the median value and the first and third quartiles (upper and lower boxes). The whiskers show the interquartile range. Dots show the mean values per replicate Petri dish (A–D, G, H) or for individual aphids (E, F).

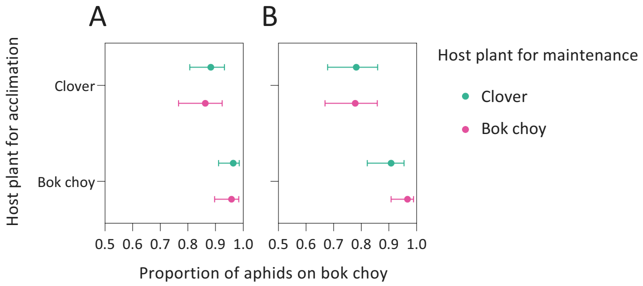

FIGURE 5 Effects of host plant and *Rickettsiella* on the proportion of aphids found on bok choy in two-choice Petri dish experiments with bok choy and clover leaf discs. Aphids from the *Rickettsiella* (–) (A) and *Rickettsiella* (+) (B) lines were maintained on clover or bok choy leaf discs for 15 generations, then acclimated on clover or bok choy for 4–5 day prior to two-choice experiments. Dots show the proportion of individuals found on bok choy after 24 h from 10 to 15 individuals per Petri dish with 10 replicates per treatment, and the error bars represent 95% binomial confidence intervals. Aphids that were not found on either leaf disc were excluded from the analysis.

maintenance plant, test plant and aphid line (Tables S6–S9), we did find an interaction between test plant and aphid line ($F_{2,192} = 8.422$, $p < 0.001$), where the cost of *Rickettsiella* to longevity appeared less pronounced when aphids were tested on potato (Figure 4C,D).

Acclimation alters host plant preferences

We then tested to see whether aphids maintained on bok choy or clover and followed by rearing on either host plant experienced a shift in host plant preferences using two-choice Petri dish experiments. Overall, aphids were overwhelmingly found on bok choy over clover leaf discs after 24 h when aphids were provided with both host plants (Figure 5). The host plant that aphids were acclimated on prior to the experiment had a significant effect on preference (generalized linear model: Wald $\chi^2 = 23.350$, df = 1, $p < 0.001$), where aphids acclimated on clover shifted their preference towards clover but still had an overall preference for bok choy (Figure 5). There were no significant effects of maintenance plant or aphid line nor any significant two-way interactions (Table S10), suggesting that the host plant used for maintenance in the previous 15 generations and *Rickettsiella* infection had little influence on host plant preferences.

DISCUSSION

Our experiments show that the fitness effects of rearing on leaf discs of different host plants and plant preferences are influenced mainly by the test host plant where the aphids develop rather than cross-generational effects. Maintenance of *M. persicae* on bok choy, clover or potato in previous generations had no effect on most traits, with clear cross-generational effects only seen for survival to adulthood and wing formation. Past studies have identified some facultative endosymbionts that differentially affect aphid performance on different host plants (Lenhart & White, 2020; Leonardo & Muiru, 2003), even when these endosymbionts are transferred to different aphid clones or species (Ferrari et al., 2007; Tsuchida et al., 2011). Here, we found limited evidence to suggest that transinfected *Rickettsiella* differentially influence aphid performance across host plants or have a role in host plant adaptation.

We found that *M. persicae* aphids transferred to clover from rearing on bok choy or potato in the previous generations experienced a decrease in survival to adulthood (Figure 3A,B). This effect was specific to aphids transferred to clover from a different host plant and not a general cross-generational maintenance effect since survival was high when aphids were tested on bok choy and potato regardless of maintenance plant. The reduced survival following a shift to clover did not translate to decreased performance in other traits or an increase in the production of winged adults (Figure 3C,D), which might have been expected if bok choy and potato were poorer hosts. Instead, these aphids may have died seeking an alternative host rather than from plant-induced mortality. This is consistent with our two-choice experiments which show a strong preference of *M. persicae* for bok choy over clover despite aphids performing equally well on the two host plants, at least in our Petri dish laboratory assays. Acclimation to clover also increased preferences for clover, which likely explains why aphids that were reared on clover in both generations had much higher survival than aphids transferred to clover from a different plant in the previous generations. Shifts in preferences following acclimation have also been observed in other aphids (Gorur et al., 2007; McLean et al., 2009).

Although wing formation (adult alates) was mainly influenced by the test plant, we also found cross-generational effects, where aphids reared on potato had a relatively high frequency of wing formation, but this remained low if they were reared on bok choy in the previous generations. Wing formation can be triggered by conditions experienced during the early instars of development as well as the parental and grandparental generations (Johnson & Birks, 1960; Lees, 1961), which can include host plant shifts (Braendle et al., 2006). Our results here show that both host plant species and shifts between hosts across generations affect the frequency of wing formation, with similar patterns experienced by both *Rickettsiella* (−) and (+) aphids which were maintained independently.

Past studies in *Myzus* species involving rearing on different host plants across generations and host plant shifts have identified maternal effects of host plant on performance (Li et al., 2015; Olivares-Donoso et al., 2007; Ramsey et al., 2014). Beyond the survival effects described above, we found no evidence for maternal effects on the investigated fitness components or any evidence for improved performance on the maintenance plant across generations. The lack of maternal effects of host plant here is consistent with some studies in other aphid species (e.g. McLean et al., 2009; Slater et al., 2019) which only identify effects of within-generation host acclimation on fitness and not effects of maternal host plant. While the presence of intraspecific variation in host plant preferences and performance suggests that populations of aphids could be selected for increased fitness on a given host plant in the long term (Nikolakakis et al., 2003), the clonal reproduction in these aphid lines, low population sizes and strong performance on all three hosts provided limited opportunities for selection and thereby evolutionary adaptation. Thus, the survival effects noted above are likely to reflect maternal or epigenetic effects rather than genetic changes in the host. However, we acknowledge that since aphid fitness can vary depending on host plant quality (e.g. Stadler et al., 2002), our experiments involving aphids maintained and tested on excised leaves may not reflect outcomes on whole plants. We also note that the use of leaf discs and frequent replacement leads to a design that ignores host plant responses to aphid infestation. Given that aphid feeding can alter plant resource allocation (Hackett et al., 2013) and trigger plant immunity responses (Jaouannet et al., 2014), future experiments should consider whether this may lead to additional host plant-specific effects on aphid fitness within and across generations.

Bacteria in the *Rickettsiella* genus are typically pathogenic (Bouchon et al., 2011) and the strain that occurs as a maternally inherited endosymbiont in aphids tends to have deleterious effects (Gu et al., 2023; Tsuchida et al., 2014). Maternally inherited endosymbionts are expected to evolve towards reduced host fitness costs to increase their persistence in populations (Perreau et al., 2021; Turelli, 1994), which may occur through genetic changes in the host and/or endosymbiont (e.g. Weeks et al., 2007). This may be particularly rapid following transfer to a novel host (McGraw et al., 2002). The persistence of fitness costs is critical for potential field applications of *Rickettsiella*, which aim to suppress the target aphid population (Gu et al., 2023). When comparing experiments performed on bok choy, the substantial costs of *Rickettsiella* have persisted for at least 3 years and around 75 generations since the infection was transferred from *A. pisum* in September 2020 (relative fecundity of *Rickettsiella* (+) compared with *Rickettsiella* (−): 0.41 in July 2021—Gu et al., 2023, 0.65 in August 2022—Ross et al., 2024 and 0.65 in September 2023—this study). However, in contrast to Ross et al. (2024), we found that longevity costs were less pronounced on potato compared with bok choy, highlighting that measures of relative fitness can be quite variable. While we did not measure endosymbiont densities directly here, *Rickettsiella* transmission and its other phenotypic effects have likely remained stable, with effects on body colour persisting in all replicate lines across the different host plant treatments.

Our finding that test plant effects dominate over cross-generational effects may have practical applications. Maintaining aphids collected from one host plant on a different host plant, or shifting host plants between maintenance and experiments may not pose an issue for aphid performance, in contrast to many sexual insect species where laboratory adaptation to artificial rearing conditions is a concern (Hoffmann & Ross, 2018). Acclimation could potentially be utilized in applied settings where transinfected aphids are intended for release onto a less favoured host plant; mass rearing on this target plant for a generation may increase the likelihood of establishment, even when a more favourable host is used to build up aphid populations. Nevertheless, it is worth considering the behaviour of this infection in other genetically different clones in the future so that genetic, cross-generational and within-generational host plant effects can be further separated.

AUTHOR CONTRIBUTIONS

Perran A. Ross: Conceptualization; formal analysis; investigation; visualization; writing – original draft; writing – review and editing. **Ella Yeatman:** Investigation; writing – review and editing. **Xinyue Gu:** Investigation; writing – review and editing. **Alex Gill:** Investigation; writing – review and editing. **Torsten N. Kristensen:** Funding acquisition; supervision; writing – review and editing. **Ary A. Hoffmann:** Formal analysis; funding acquisition; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that no competing interests exist.

DATA AVAILABILITY STATEMENT

Raw data will be provided on request.

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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. General linear model for hue (Figure 2A).

Table S2. General linear model for saturation (Figure 2B).

Table S3. General linear model for lightness (Figure 2C).

Table S4. Generalized linear model for the proportion of aphids reaching adulthood (Figure 3A,B).

Table S5. Generalized linear model for the proportion of adult aphids that developed into alates (Figure 3C,D).

Table S6. General linear model for fecundity (Figure 4A,B).

Table S7. General linear model for longevity (Figure 4C,D).

Table S8. General linear model for body length (Figure 4E,F).

Table S9. General linear model for total productivity (Figure 4G,H).

Table S10. Generalized linear model for the proportion of aphids found on bok choy in two-choice experiments (Figure 5).

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