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LETTER

Use of an exotic host plant reduces viral burden in a native insect herbivore

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Abstract

Incorporation of exotic plants into the diets of native herbivores is a common phenomenon, influencing interactions with natural enemies and providing insight into the tritrophic costs and benefits of dietary expansion. We evaluated how use of an exotic plant, *Plantago lanceolata*, impacted immune performance, development and susceptibility to pathogen infection in the neotropical herbivore *Anartia jatrophae* (Lepidoptera: Nymphalidae). Caterpillars were reared on *P. lanceolata* or a native plant, *Bacopa monnieri*, and experimentally infected with a pathogenic virus, Junonia coenia densovirus. We found that virus-challenged herbivores exhibited higher survival rates and lower viral burdens when reared on *P. lanceolata* compared to *B. monnieri*, though immune performance and development time were largely similar on the two plants. These findings reveal that use of an exotic plant can impact the vulnerability of a native herbivore to pathogen infection, suggesting diet-mediated protection against disease as a potential mechanism facilitating the incorporation of novel resources.

KEYWORDS

Anartia jatrophae, *Bacopa monnieri*, diet breadth, entomopathogens, immune response, Junonia coenia densovirus, larval performance, natural enemies, *Plantago lanceolata*, tritrophic interactions

INTRODUCTION

Species introductions are a pervasive phenomenon in the modern world, driving substantial ecological and evolutionary change for native species (Mack et al., 2000; Strauss et al., 2006). Exotic plants, in particular, can alter the structure of existing communities and give rise to novel trophic interactions when adopted into the diets of native herbivores (Bezemer et al., 2014; Sunny et al., 2015). For many insect herbivores, exotic plants represent toxic or inferior resources compared to native plants (Yoon & Read, 2016) and may act as 'evolutionary traps' for those that colonise them (Keeler & Chew, 2008; Schlaepfer et al., 2005). Alternatively, exotic plants may provide suitable niches for native herbivores and can facilitate population growth or geographical range expansion (Brown et al., 2017; Graves & Shapiro, 2003). As the incorporation of exotic plants into native diets increases (e.g. Shapiro, 2002), characterising the consequences of such dietary expansion for herbivore ecology and evolution is paramount for understanding the ongoing impacts of introduced species on ecosystems (Tallamy et al., 2021).

Most research on the consequences of exotic plant use has focused on differences in oviposition preference and larval performance on native versus exotic plants (e.g., Bowers et al., 1992; Forister et al., 2009; Keeler & Chew, 2008). A meta-analysis by Yoon and Read (2016) revealed reductions in body mass and survival in Lepidoptera using exotic plants, indicating that dietary expansion may frequently entail costs for herbivore performance. However, herbivore fitness on exotic plants is context-dependent and influenced by many factors beyond suitability for development, including multitrophic

interactions (Forister et al., 2020; Price et al., 1980). Consideration of such interactions, alongside development and reproduction, may provide more comprehensive insight into the fitness outcomes of colonising exotic plants.

Natural enemies, including microbial pathogens, are significant agents of mortality for insect herbivores (Hawkins et al., 1997) and can exert differential pressure on populations utilising native and exotic plants (Feder, 1995; Grosman et al., 2017). Importantly, even if an exotic plant supports relatively poor herbivore development, its use may be advantageous if it provides enemy-free space (Bernays & Graham, 1988; Jeffries & Lawton, 1984). For example, exotic plants may be associated with reduced frequency of enemy attack (Fortuna et al., 2013) or may enhance the degree to which herbivores can defend themselves. While the importance of incorporating tritrophic interactions into the study of herbivore diet breadth has been recognised (Harvey et al., 2010; Lill et al., 2002; Singer & Stireman, 2005), few studies have investigated the role of natural enemies in shaping herbivore fitness on exotic plants, in particular (Fortuna et al., 2013). Fewer still have focused on interactions with entomopathogens, compared to predators or parasitoids, representing a critical knowledge gap.

Substantial research has shown that interactions between insect herbivores and pathogens can vary dramatically based on host plant use (Cory & Hoover, 2006). Herbivore mortality can vary up to 100-fold when viral or bacterial pathogens are ingested on different plant species (Ali et al., 1998; Kouassi et al., 2001), and metrics including speed-of-kill and pathogen yield may also differ (Raymond et al., 2002). Such variation may be mediated by direct interactions between plants and pathogens (e.g., in the midgut; Felton & Duffey, 1990) or indirect interactions mediated by herbivore physiology (Shikano et al., 2010). Use of exotic plants, which may differ from native plants in macronutritional composition, secondary chemistry and a variety of other traits, may therefore be expected to impact vulnerability to pathogens in many cases.

One physiological route through which host plant use can impact herbivore susceptibility to pathogens is through effects on immune performance (Smilanich & Muchoney, 2022). Use of different host plants can give rise to significant variation in herbivore immune function (Carper et al., 2019; Diamond & Kingsolver, 2011; Shikano et al., 2010), which may contribute to the ability, or inability, of certain plants to provide enemy-free space (Muller et al., 2015). Although considerable progress has been made in documenting the effects of host plant use on entomopathogen infection, relatively few studies have characterised the role of the immune response in mediating these interactions, or the outcomes of diet-mediated variation in infection and immunity for reproduction (i.e., sublethal effects). Characterising the effects of exotic host plants on herbivore resistance to pathogens, immune performance *and* reproduction offer potential for insight into the multifaceted costs and benefits of dietary expansion.

In this study, we investigated the tritrophic consequences of exotic plant use for a native herbivore, *Anartia jatrophae* L. (Lepidoptera: Nymphalidae). This species appears to be in the early stages of incorporating an exotic plant, *Plantago lanceolata* L. (Plantaginaceae), into its host range, and exhibits differential performance (slower development, but larger pupae) when reared on this plant compared to a native host, *Bacopa monnieri* (L.) Pennell (Plantaginaceae) (Knerl & Bowers, 2013). Here, we report that this herbivore can also be infected by a naturally occurring pathogen of Lepidoptera, Junonia coenia densovirus (*Parvoviridae*). We surveyed wild populations of *A. jatrophae* to determine viral prevalence and then performed a factorial experiment to evaluate how consuming *P. lanceolata* mediates *A. jatrophae* performance through changes in response to viral infection. We addressed two questions: (1) Does exotic plant use impact herbivore immune function and/or vulnerability to viral infection? and (2) Does host plant use mediate the impacts of viral infection on herbivore development, survival, oviposition preference and fecundity? Based on previous research, we predicted that the exotic plant would suppress herbivore immunity (Smilanich et al., 2009) but enhance protection against viral infection (Muchoney et al., 2022) due its distinct chemistry (see below). By simultaneously evaluating herbivore immune function, susceptibility to a natural pathogen and performance, we provide insight into the tritrophic outcomes of host range expansion.

METHODS

Herbivore, host plants and virus

Anartia jatrophae is a neotropical butterfly distributed throughout the southern United States, West Indies, Central America and much of South America (Pfeiler et al., 2020; Silberglied et al., 1979). Caterpillars of this species have been recorded using host plants from five families (Knerl & Bowers, 2013). In Florida, their primary host plant is *Bacopa monnieri* (hereafter, *Bacopa*), a perennial herb commonly found in wetlands (Rawson, 1976). Recently, *A. jatrophae* caterpillars in Florida were observed consuming an exotic plant, *Plantago lanceolata* (hereafter, *Plantago*) (Knerl & Bowers, 2013), a perennial herb introduced to North America from Europe during the 1800s (Cavers et al., 1980). This plant has since become widespread and has been incorporated into the diets of several North American lepidopterans (Bowers et al., 1992; Haan et al., 2021; Singer & Parmesan, 2018; Thomas et al., 1987).

Previous research showed that *A. jatrophae* took longer to develop on *Plantago* versus *Bacopa*, but

exhibited higher pupal weights (Knerl & Bowers, 2013). Importantly, these plants differ in their secondary chemistry, which may influence herbivore interactions with enemies. *Plantago* contains iridoid glycosides (IGs), monoterpenoid metabolites that can be toxic and/or deterrent to non-adapted herbivores (Abate et al., 2022; Bowers & Puttick, 1988; Miehe-Steier et al., 2015). *Anartia jatrophae* larvae are capable of sequestering and retaining small amounts of IGs into the pupal and adult stages (Knerl & Bowers, 2013), which provide chemical defence in other sequestering species (Bowers, 1993). However, sequestration of high concentrations of IGs has also been associated with suppression of lepidopteran immune responses (Smilanich et al., 2009; Lampert & Bowers, 2015). In contrast, *Bacopa* contains no IGs, but contains a variety of other secondary compounds (Basak et al., 2016), none of which are known to be sequestered.

Junonia coenia densovirus (hereafter, JcDV), is a nonenveloped, single-stranded DNA virus in the family *Parvoviridae* (*Densovirinae: Lepidopteran protoambidensovirus 1*) capable of infecting lepidopterans from multiple families (Mutuel et al., 2010; Rivers & Longworth, 1968; Smilanich et al., 2018). Caterpillars are infected by JcDV via ingestion of viral particles, and the pathogen crosses the midgut to replicate in tracheae, haemocytes, visceral muscles and epidermis (Wang et al., 2013). Infection can result in hypoxia, disruptions to moulting and metamorphosis and mortality (Mutuel et al., 2010). Notably, JcDV infection may be influenced by consumption of IGs: a recent study found that higher levels of IG sequestration were associated with reduced JcDV loads in another butterfly, *Euphydryas phaeton* (Nymphalidae) (Muchoney et al., 2022).

Field survey

To determine whether *A. jatrophae* encounters JcDV in the wild, we collected butterflies ($n = 95$) from seven locations in Florida in April 2017 (Appendix S1: Table S1). Though host plant use during the larval stage was not observed, the native *Bacopa* was present at all locations, while the exotic *Plantago* was not observed and has not been recorded in the counties from which butterflies were collected (USDA 2021) (but see Figure S1 for distribution overlap). Butterflies were sent live to University of Colorado, Boulder, where females oviposited to establish a colony. Following death, butterflies were frozen and screened for JcDV.

Viral screening

To detect JcDV in wild-collected butterflies, wings were removed, and total DNA was extracted from remaining tissues using Qiagen DNeasy 96 Blood and Tissue Kits (Qiagen, Hilden, North Rhine-Westphalia, Germany) following the manufacturer's protocol. Extracted DNA was screened for JcDV using quantitative PCR following the protocols of Muchoney et al. (2022), with primers specific to the VP4 gene of JcDV (Wang et al., 2013) and 28S rDNA primers (Nice et al., 2009) as an internal control. Samples were screened in duplicate for the VP4 gene and singly for the 28S gene using iTaq Universal SYBR Green Supermix (Bio-Rad, Hercules, CA, USA) with a Bio-Rad CFX96 Optics Module and C1000 Thermal Cycler.

Viral sequencing

To examine similarities between JcDV detected in *A. jatrophae* and the laboratory-propagated isolate used in the following experiment (originally isolated from *Junonia coenia*, Nymphalidae), we sequenced the VP4 capsid protein gene of JcDV. Briefly, butterfly DNA found to contain JcDV via qPCR underwent nested PCR using external and internal primers for the VP4 gene, which were designed for this study based on the published genome for JcDV (GenBank: KC883978; Pham et al., 2013). PCR products were resolved using agarose gel electrophoresis, purified using QIAquick PCR Purification Kits (Qiagen) and submitted to the Nevada Genomics Center for Sanger sequencing. Sequences were trimmed and aligned using Unipro UGENE (Okonechnikov et al., 2012) and sequence identity (%) with the JcDV 'Oxford' isolate was evaluated. See Appendix S1 for details.

Laboratory experiment

Overview

To investigate how host plant use impacts *A. jatrophae*'s vulnerability to JcDV, we conducted a factorial experiment in which caterpillars were reared in the laboratory on either the native *Bacopa* or the exotic *Plantago*. Upon reaching the final larval instar, a subset of each group was orally inoculated with JcDV, and a subset of each resulting group underwent immune assays (Figure 1). Caterpillars were then reared to mortality or adulthood to evaluate the effects of host plant use and viral challenge on development and survival. Those that reached the adult stage underwent mating and oviposition trials to assess fecundity and oviposition preference.

Dietary treatments

Descendants of *A. jatrophae* collected from Florida ($n = 75$) were used to establish a colony of mixed parentage at University of Nevada, Reno in September/October 2017. After hatching, first instar caterpillars were housed in 1 oz plastic cups and randomly assigned

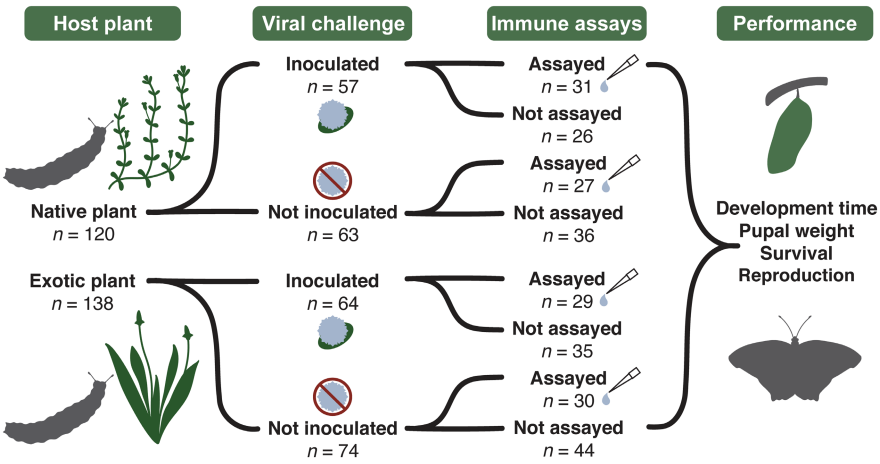

FIGURE 1 Factorial experiment designed to investigate the effects of exotic host plant use and viral infection on *Anartia jatrophae* development, immune function, survival and reproduction. Caterpillars were reared in the laboratory on either the native plant, *Bacopa monnieri*, or the exotic *Plantago lanceolata*. Upon reaching the final larval instar, approximately half of each group was orally inoculated with Junonia coenia densovirus, and 4 days later, a subset of each resulting group underwent immune assays (haemocyte counts and melanisation of an abiotic implant). Caterpillars were then reared to mortality or adulthood to evaluate effects of host plant use and viral challenge on development time, pupal weight and survival. Those that reached the adult stage underwent mating and oviposition trials to assess fecundity and oviposition preference.

to feed on either *Bacopa* or *Plantago* throughout larval development (Figure 1). Caterpillars were reared in incubators using a 16 L:8D photoperiod (day temperature: 25°C, night temperature: 20°C) and fed ad libitum with foliage grown in a hydroponics system. Upon moulting to the third instar, caterpillars were transferred to individual 2 oz plastic cups and dates of moulting, pupation, and eclosion were recorded. See Appendix S1 for details.

Viral challenge

On the day following moulting to the sixth instar, approximately half of each host plant group was randomly selected to be orally inoculated with JcDV (Figure 1). Caterpillars were presented with an 8 mm leaf disc (*Bacopa* or *Plantago*, according to group) with 10^7 viral particles suspended in 1 µl of water pipetted onto the surface. Caterpillars were given 24 h to consume the disc, and those that did not were excluded from the experiment (n = 18; not included in Figure 1). Following inoculation, virus-challenged individuals were maintained at a separate location from controls to prevent cross-contamination.

Immune assays

To evaluate effects of host plant and viral challenge on herbivore immunity, random subsets of all groups underwent immune assays on the fifth day of the sixth instar (Figure 1). We measured two parameters: haemocyte concentrations in the haemolymph and the melanisation response against an abiotic implant. Briefly, haemolymph was extracted from caterpillars and haemocytes were counted following the protocol of Muchoney et al. (2022). A 2 mm nylon monofilament was then inserted into the wound created during haemolymph extraction, and caterpillars were given 24 h to react to this implant. Following removal, implants were photographed to quantify their degree of melanisation. See Appendix S1 for details.

Pupation and oviposition

Following immune assays, caterpillars were reared to mortality or adulthood. Pupae were weighed, and butterflies were assigned to mating groups (one female/two males) within their treatment groups. These were housed together in 5 L plastic containers and maintained on 10% honey water for at least 3 days to allow for mating. Females were then transferred to individual 5 L containers containing two plants (*Bacopa* and *Plantago*) housed in 2 oz cups and allowed to oviposit for 3–4 days. Oviposition preference index (OPI) is presented as the proportion of eggs laid on *Bacopa* [(*Bacopa* eggs—*Plantago* eggs)/total], with OPI = 1 representing total preference for *Bacopa* and OPI = −1 representing total preference for *Plantago* (Keeler & Chew, 2008).

Viral screening

To quantify post-mortem JcDV loads of virus-challenged individuals and verify the absence of JcDV in unchallenged controls, DNA was extracted from tissue samples from each individual and screened for JcDV using the protocols above. Whole butterflies (wings removed) and pupae were used for DNA extractions, whereas an

aliquot of homogenised tissue was used for each larva. Viral loads were calculated as $2^{-\Delta Ct}$ (Schmittgen & Livak, 2008), representing the abundance of the JcDV gene relative to the abundance of the internal control gene [ΔC_t = mean C_t (threshold cycle) for VP4 – C_t for 28S] and log-transformed.

Statistical analyses

Statistical analyses were performed in R version 4.0.4 using the 'stats' and 'car' packages (Fox & Weisberg, 2019; R Core Team, 2021). Effects of host plant (*Bacopa*/*Plantago*), viral treatment (JcDV-challenged/control) and their interaction on survival to adulthood (Y/N) were evaluated using logistic regression. As the process of assessing immunity reduced survival, immune assay status (assayed/not) was also included as a predictor. Within individuals that were inoculated with JcDV, the relationship between post-mortem viral detection (presence/absence of JcDV) and survival was examined using logistic regression with host plant, viral detection and assay status as predictors and survival as the response. Post-mortem JcDV loads were compared using multiple regression with host plant, survival and assay status as predictors, and the relationship between viral load and survival was assessed using logistic regression with viral load, host plant, their interaction and assay status as predictors and survival as the response.

Pre-inoculation development time, defined as the days between moulting to the third instar and the second day of the sixth instar (when inoculation occurred), was compared based on host plant and treatment group assignment (to confirm the absence of bias) using two-way ANOVA. Effects of host plant and viral treatment on post-inoculation development time (days between inoculation and eclosion), pupal time (days in pupal stage) and pupal weight were assessed using separate multiple regressions that included the covariate of immune assay status. The pupal weight model additionally included sex as a predictor due to observed dimorphism in size.

Immune responses (square-root transformed haemocyte concentration and squared melanisation score) were compared across host plants and viral treatments using separate two-way ANOVAs. The outcomes of immune variation for survival of virus-challenged insects were assessed using logistic regressions that included host plant and either haemocyte concentration or melanisation as predictors, while relationships between immunity and post-mortem viral loads were assessed using multiple regressions with the same predictors. Female fecundity (eggs laid over 3–4 days) and oviposition preference (OPI) were examined using separate multiple regressions, which included host plant and viral treatment as predictors and number of oviposition days as a covariate.

RESULTS

Field survey

Junonia coenia densovirus was detected in wild *A. jatrophae* butterflies originating from six out of seven sampling locations at an overall frequency of 12% ($n = 11$ out of 95). Sequences for the VP4 structural protein gene of JcDV from wild-collected *A. jatrophae* ($n = 4$) exhibited 99.8%–100% identity with the published genome for this pathogen (Figure S2) (Pham et al., 2013), indicating high similarity between wild isolates of JcDV occurring in *A. jatrophae* populations and the laboratory-propagated isolate utilised for experimental inoculations in this study. See Appendix S1 for details on viral prevalence and sequencing.

Laboratory experiment

Survival

Host plant species did not significantly impact survival to the adult stage in individuals that were not inoculated with the virus (Figure 2) (odds ratio [OR] = 1.95, 95% confidence interval [CI] = [0.66–6.10], $z = 1.2$, $p = 0.2$). However, there was a significant interaction between host plant and viral treatment on survival, revealing

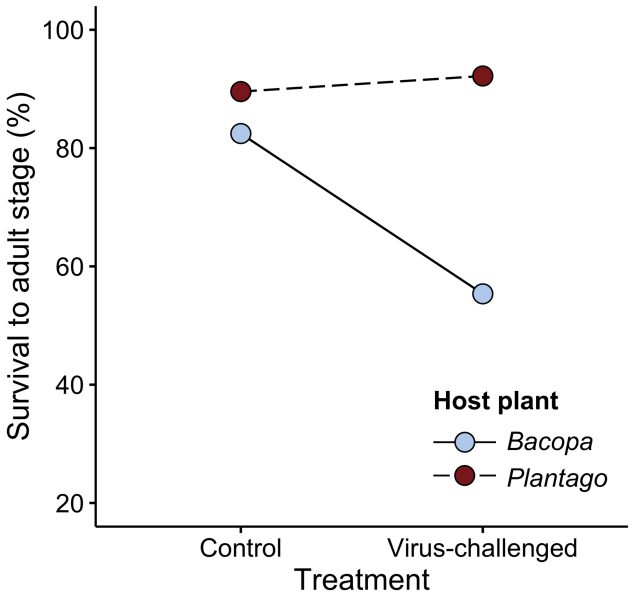

FIGURE 2 Effects of larval host plant species and viral treatment on survival of *Anartia jatrophae* to the adult stage. Individuals reared on the native host plant, *Bacopa monnieri*, exhibited a reduced frequency of survival to adulthood when inoculated with Junonia coenia densovirus during the final larval instar ($n = 56$), compared to unchallenged controls ($n = 57$). In contrast, individuals reared on the exotic host plant, *Plantago lanceolata*, exhibited similarly high survival rates across treatment groups (virus-inoculated: $n = 64$; unchallenged controls: $n = 67$).

that survival of JcDV challenge was dependent upon host plant (Figure 2) (host plant x treatment: OR = 5.73, 95%CI = [1.21–29.01], $z = 2.2$, $p = 0.03$). Specifically, virus-inoculated caterpillars reared on *Plantago* had 11 times greater odds of surviving compared to inoculated caterpillars reared on *Bacopa* (Table S2).

Viral detection and loads

Of individuals inoculated with JcDV, 57% harboured a detectable infection at death, indicating that the remaining 43% were able to either avoid, clear or suppress infection below detectable levels. The likelihood of JcDV detection did not differ based on host plant (Figure 3a) ($X^2 = 0.03$, $df = 1$, $p = 0.9$). The absence of a detectable infection was associated with high survival on both plants (Figure 3b), while detection of JcDV was associated with increased mortality in the larval or pupal stage (OR = 0.08, 95%CI = [0.02–0.31], $z = -3.4$, $p = 0.001$).

Within individuals that maintained a detectable infection at death, viral loads were over 200-fold higher in those reared on *Bacopa*, compared to *Plantago* (Figure 3c). This pattern was primarily mediated by higher frequency of survival on *Plantago*, as viral loads were substantially lower in individuals that reached the adult stage, compared to those that died as larvae or pupae ($\beta = -3.78 \pm 0.68$, $t = -5.5$, $df = 57$, $p < 0.0001$). In addition, there was a significant negative relationship between viral load and probability of survival to adulthood within individuals reared on *Bacopa* (Figure 3d) (OR = 0.09, 95%CI = [0.00–0.41], $z = -2.0$, $p = 0.04$). In contrast, 100% of individuals that were reared on *Plantago* and did not undergo immune assays survived inoculation with JcDV. Thus, when accounting for the effect of immune assessment, we documented 0% mortality on *Plantago* following JcDV challenge, regardless of viral burden.

Development

Pre-inoculation development time did not differ between caterpillars consuming *Bacopa* and *Plantago* ($F_{1,247} = 0.26$, $p = 0.6$). Following inoculation, the time

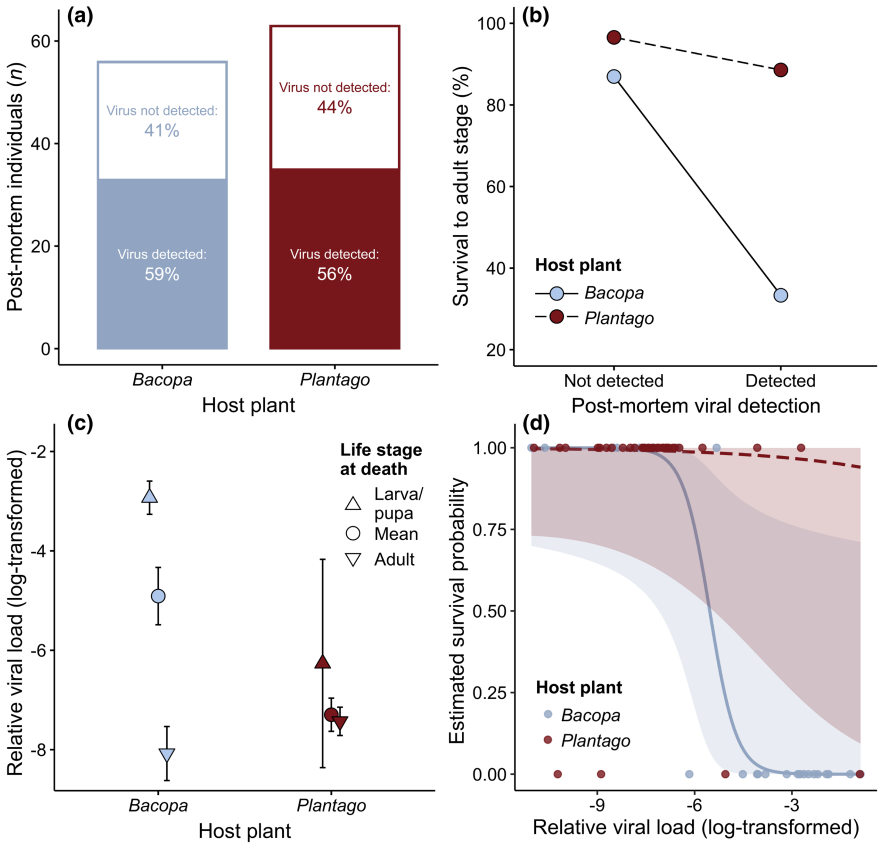

FIGURE 3 Effects of larval host plant species on infection and resistance parameters in *Anartia jatrophae* inoculated with Junonia coenia densovirus. (a) Post-mortem detection frequencies of JcDV in individuals reared on either the native plant, *Bacopa monnieri*, or the exotic *Plantago lanceolata*. (b) Frequencies of survival to the adult stage based on post-mortem detection of JcDV and host plant. (c) Post-mortem viral loads of individuals reared on *Bacopa* and *Plantago*. Points represent mean ± SE and are provided for individuals that died prior to reaching the adult stage (larva/pupa) and those that survived to reach the adult stage (adult), along with the overall means for each host plant group. (d) Relationship between post-mortem viral load and estimated survival probability in individuals reared on *Bacopa* or *Plantago*. Points represent individuals.

required to reach the adult stage (final instar to eclosion) again did not differ based on host plant ($\beta = 0.16 \pm 0.18$, $t = 0.90$, $df = 172$, $p = 0.4$), but was accelerated by an average of 1.3 days in virus-challenged individuals compared to controls ($\beta = -1.31 \pm 0.18$, $t = -7.3$, $df = 172$, $p < 0.0001$) (Table S3). When examining duration of the pupal stage in particular, an interaction between host plant and viral treatment emerged (Figure 4a) ($\beta = -0.72 \pm 0.24$, $t = -3.1$, $df = 171$, $p = 0.002$). Control individuals reared on *Plantago* spent significantly more time as pupae than those reared on *Bacopa*, but also exhibited a decrease in pupal time when inoculated with JcDV, whereas those reared on *Bacopa* did not. Thus, dietary effects on pupal development varied depending on viral exposure.

Pupal weights were significantly higher in individuals reared on *Plantago*, compared to those reared on *Bacopa* (Figure 4b) ($\beta = 19.2 \pm 6.4$, $t = 3.0$, $df = 175$, $p = 0.003$). In addition, there was a negative effect of viral inoculation on pupal weight ($\beta = -27.6 \pm 6.4$, $t = -4.3$, $df = 175$, $p < 0.0001$). When accounting for the effects of immune assessment and sexual dimorphism (Table S3), pupal weights were on average 7% greater in individuals reared on *Plantago* than *Bacopa* and 10% greater in unchallenged controls than JcDV-inoculated individuals.

Immune responses

Haemocyte concentrations did not differ significantly between caterpillars reared on *Bacopa* and *Plantago* (Figure 5a) ($F_{1,90} = 0.64$, $p = 0.4$). However, JcDV-challenged caterpillars exhibited reduced haemocytes relative to controls on both plants ($F_{1,90} = 4.0$, $p = 0.05$). Similarly, inoculation with JcDV reduced the strength of the melanisation

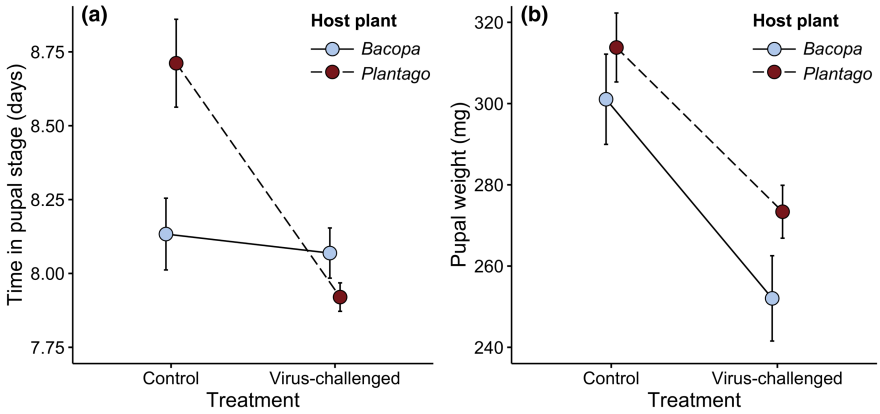

FIGURE 4 Effects of larval host plant species and inoculation with Junonia coenia densovirus on pupal development time and pupal weight in *Anartia jatrophae*. Points represent mean±SE. (a) Unchallenged controls reared on the native plant, *Bacopa monnieri*, exhibited faster pupal development than those reared on the exotic plant, *Plantago lanceolata*. However, pupal development time was similar across the two host plants in virus-inoculated individuals. (b) Pupal weight was greater in individuals reared on *Plantago* than those reared on *Bacopa* when accounting for the effects of immune assessment and sexual dimorphism in body size (see Table S3), and was additionally reduced in virus-inoculated individuals, relative to unchallenged controls, on both host plants.

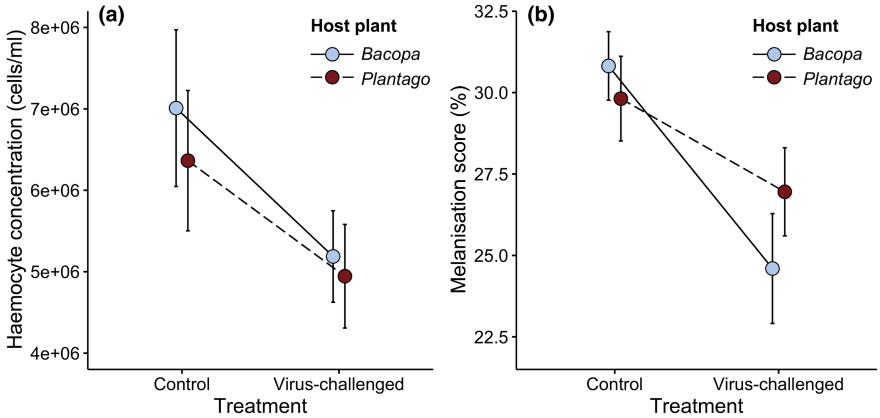

FIGURE 5 Immune responses of *Anartia jatrophae* caterpillars based on larval host plant species and inoculation with Junonia coenia densovirus. Points represent mean±SE. (a) Haemocyte concentrations in the haemolymph did not differ between caterpillars reared on the native *Bacopa monnieri* and the exotic *Plantago lanceolata*. However, caterpillars that were inoculated with JcDV exhibited reduced haemocyte concentrations, relative to unchallenged controls. (b) Melanisation of an abiotic implant (nylon monofilament) did not differ based upon host plant use, while inoculation with JcDV had a negative impact on melanisation score across both host plant groups.

response (Figure 5b) ($F_{1,97}$ = 9.1, p = 0.003), but there was no significant effect of host plant on this parameter ($F_{1,97}$ = 0.21, p = 0.6). Neither haemocyte concentration nor melanisation score was significantly associated with survival following viral challenge (Table S4). However, viral loads were greater in individuals with higher melanisation scores on *Bacopa* (β = 0.0032 ± 0.0015, t = 2.1, df = 27, p = 0.04), which may indicate increased activation of this response in reaction to higher viral burdens.

Oviposition and fecundity

Females exhibited a strong preference for oviposition on the native *Bacopa* compared to *Plantago* (mean OPI = 0.996 ± 0.004, n = 31), regardless of the plant upon which they were reared (β = −0.012 ± 0.010, t = −1.3, df = 27, p = 0.2). There were no successful oviposition trials involving JcDV-challenged females reared on *Bacopa*, likely due to the low number of surviving adults in this group; however, viral treatment did not significantly influence OPI in individuals reared on *Plantago* (β = 0.0099 ± 0.0093, t = 1.1, df = 27, p = 0.3). Only two females laid any eggs on *Plantago*; both had been reared on *Plantago*, and in both cases, the eggs laid on *Bacopa* (n = 91, 49) outnumbered the eggs laid on *Plantago* (n = 1, 3). Fecundity, measured as total eggs laid, also did not differ based on host plant (Figure 6) (β = 3.2 ± 12.2, t = 0.26, df = 27, p = 0.8) or viral treatment (β = −1.3 ± 11.6, t = −0.11, df = 27, p = 0.9).

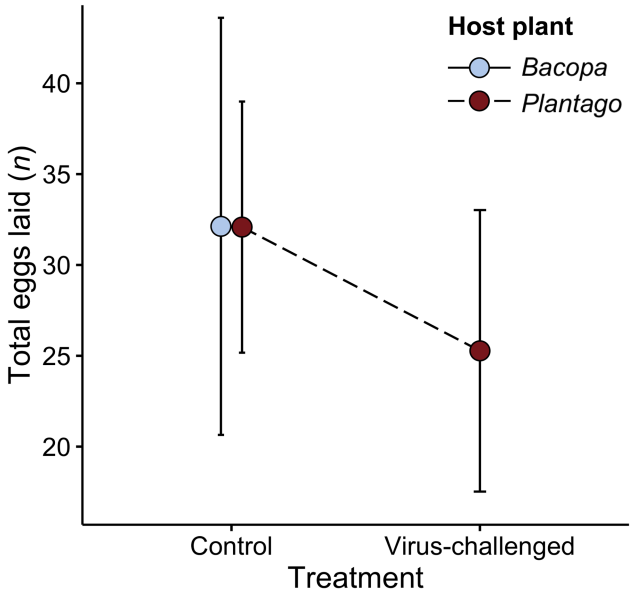

FIGURE 6 Effects of larval host plant species and inoculation with Junonia coenia densovirus on fecundity of *Anartia jatrophae* females. Points represent mean ± SE. The total number of eggs laid over 3–4 days did not differ significantly between unchallenged controls that were reared on the native plant, *Bacopa monnieri*, or the exotic plant, *Plantago lanceolata*. In addition, the number of eggs laid by females reared on *Plantago* were similar across virus-inoculated individuals and controls. There were no successful oviposition trials involving virus-inoculated individuals that were reared on *Bacopa*, likely due to the low number of surviving adults within this group.

DISCUSSION

This study demonstrates that utilising an exotic plant can dramatically reduce the vulnerability of a native herbivore to pathogen infection. When reared on *Plantago*, individuals inoculated with JcDV experienced high survival (100% of individuals that did not undergo immune assays), but the odds of surviving viral challenge decreased markedly on *Bacopa* (Figure 2). The lack of virus-induced mortality in individuals reared on *Plantago* was unexpected and may be predicted to promote the incorporation of *Plantago* into the dietary range of *A. jatrophae*, particularly in populations where exposure to JcDV is high. Importantly, our preliminary survey confirmed that JcDV is present in wild *A. jatrophae* populations, and that the virus encountered by these herbivores is genetically similar to the isolate used in our experiment (Figure S2). This represents the first record of JcDV in *A. jatrophae* and the first investigation of genetic similarity between JcDV in modern butterflies and a laboratory-propagated isolate. Despite this putative benefit of *Plantago*, butterflies exhibited a strong preference for oviposition on the native *Bacopa* across treatments. However, this may be explained by the novelty of *Plantago* to the herbivore lineage used for this experiment, which originated from locations where *Plantago* is not common (Figure S1). Gaining a deeper understanding of the prevalence of JcDV throughout *A. jatrophae*'s range, and the extent to which *Plantago* confers protection against infection in field settings, will represent important steps towards understanding how this tritrophic benefit may shape the ecology and realised host range of this herbivore.

The stark difference in survivorship between individuals reared on the native and exotic plants raises the question of whether individuals consuming *Plantago* avoided the establishment of infection ('qualitative resistance'; De Roode et al., 2011) (see below). However, a similar proportion of virus-inoculated individuals showed no detectable infection when reared on the two plants (Figure 3a), suggesting that the ability to avoid infection was not plant-dependent. Whether due to avoidance or clearance, these individuals experienced higher survival, while the majority of mortality was observed in individuals that maintained detectable infections (Figure 3b). Within this cohort with detectable infections, JcDV loads were lower in individuals reared on *Plantago* (most of which survived to adulthood) compared to *Bacopa*, where loads were higher and primarily detected in larvae and pupae (Figure 3c). Thus, herbivores using the exotic plant harboured lower viral burdens by the time they died. We also documented a negative relationship between viral load and survival on

Bacopa (Figure 3d), indicating that higher viral burdens experienced by herbivores using this plant were a causal agent in their mortality. Given these patterns, it is likely that using *Plantago* provides protection against JcDV via ' quantitative resistance', or the ability to reduce pathogen burden upon infection.

Use of the exotic plant could reduce viral burdens in *A. jatrophae* through a number of mechanisms. First, ingesting JcDV on *Plantago* may decrease the effective dose of viral particles that initially establish infection via the midgut (De Roode et al., 2011). Certain phytochemicals have been found to directly interfere with viral infectivity in other lepidopterans (Felton & Duffey, 1990; Keating et al., 1990); however, if this were the case with *Plantago*, we would have expected to observe greater differences in infection probability between the two plants (Figure 3a). The second, and more likely, scenario is that consuming *Plantago* suppresses JcDV replication once infection has been established, since post-mortem viral loads were 200-fold lower on this plant (Figure 3c). As lower viral loads on *Plantago* were primarily mediated by higher survival to adulthood (Figure 3b), and JcDV is known to impair pupation (Mutuel et al., 2010), we hypothesise that individuals using this plant were better able to suppress JcDV during the larval stage, thereby increasing their chance of reaching and surviving metamorphosis.

Host plant use may indirectly influence entomopathogen burdens through impacts on herbivore development. In contrast to previous research with *A. jatrophae* (Knerl & Bowers, 2013), we found only partial evidence of slower development on *Plantago*, relative to *Bacopa*: larval development time was similar on the two plants, while pupal development was slower and pupal weights were higher on *Plantago* (Figure 4a) (see also Lampert et al., 2014). In addition, inoculation with the virus accelerated development and resulted in smaller pupae (Figure 4b). Accelerated development in response to JcDV infection has been documented in another butterfly (Smilanich et al., 2018); whether this represents an advantageous strategy on the part of the herbivore, a form of host manipulation benefitting the virus, or both, remains undetermined. If herbivores can suppress or clear JcDV through metamorphosis, then reaching eclosion quickly may maximise their chance of reproducing. Though individuals reared on *Plantago* showed accelerated pupal development in response to viral challenge (Figure 4a), they ultimately reached eclosion within a similar time to those reared on *Bacopa*, suggesting that this developmental difference was unlikely to explain the reduced viral loads documented on the exotic plant.

Another avenue through which host plant use may influence herbivore resistance to entomopathogens is through enhancement or suppression of immunity. In this study, however, variation in immunocompetence did not appear to mediate differences in vulnerability to JcDV. Both haemocyte concentrations and melanisation (Figure 5) were similar in caterpillars using *Bacopa* and *Plantago*, and neither parameter strongly predicted survival following viral challenge (Table S4). Importantly, both parameters may also contribute to defence against other enemies (e.g., parasitoids; Carton et al., 2008). Similarity in immune performance on the two plants is surprising, given their differing chemistry: *Plantago* contains iridoid glycosides, which were linked to suppression of immunity in three other lepidopterans (Lampert & Bowers, 2015; Muchoney et al., 2022; Smilanich et al., 2009). However, these species are all specialists that sequester IGs in high concentrations, whereas *A. jatrophae* sequesters lower levels of IGs (Knerl & Bowers, 2013) that may be insufficient to elicit an immunosuppressive effect.

As diet-mediated variation in development and immunity provided limited explanation, additional research will be necessary to elucidate how *A. jatrophae* reared on *Plantago* are able to suppress viral burdens and increase their likelihood of surviving infection. As the specific routes through which the immune response contributes to defence against JcDV are unclear (Muchoney et al., 2022; Resnik & Smilanich, 2020; Smilanich et al., 2018), it is possible that immune parameters that were not measured are enhanced in larvae consuming *Plantago*. In addition, the role of phytochemistry warrants consideration. As previously noted, *A. jatrophae* is capable of sequestering IGs when feeding on *Plantago* but not *Bacopa*, representing a potentially consequential physiological difference within the context of tritrophic interactions (Knerl & Bowers, 2013; Lampert et al., 2014). Research with *Euphydryas phaeton*, a nymphalid that exhibits high IG sequestration, revealed a negative relationship between sequestration and JcDV loads (Muchoney et al., 2022), suggesting that IG sequestration may contribute to, or enhance, defence against this virus.

This study provides evidence of a clear tritrophic fitness benefit that can arise through adoption of an exotic plant into the diet of a native herbivore. We discovered that consuming *Plantago* provides *A. jatrophae* with a survival advantage when faced with JcDV infection (Figure 2), though the mechanism underlying this pattern remains unclear. We found little evidence to suggest that this benefit was accompanied by fitness-related costs and conclude that *Plantago* represents: (1) a suitable resource for supporting *A. jatrophae* development in the absence of JcDV infection, and (2) a superior resource for supporting *A. jatrophae* development when JcDV is present, both of which could facilitate population growth or geographical expansion in this species. These results illustrate that host plant identity can dramatically impact herbivore–enemy interactions (Cory & Hoover, 2006; Kaplan et al., 2016). Examination of plant-mediated effects on interactions with higher trophic levels, including pathogens, may therefore offer valuable insight into the evolution of herbivore host range and the ecological impacts of exotic plants.

AUTHOR CONTRIBUTIONS

The study was conceived by AMS and MDB, and all authors contributed to experimental design. ALC and NDM conducted the field survey, and viral sequencing was performed by NDM under the guidance of MBT. NDM conducted the laboratory experiment, analysed data and wrote the article, and all authors contributed to revisions.

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DATA AVAILABILITY STATEMENT

Data and code supporting the results presented in this article are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.7pvmcvdxx) and nucleotide sequences of viral isolates are available in GenBank (accession numbers OQ116902–OQ116905).

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SUPPORTING INFORMATION

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

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