



Sub-lethal viral exposure and growth on drought stressed host plants changes resource allocation patterns and life history costs in the Speckled Wood butterfly, *Pararge aegeria*



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ABSTRACT

This study investigated the interactive effects of growth on drought stressed host plants and pathogen challenge with the baculovirus *Autographa californica nucleopolyhedrovirus* (AcMNPV) on survival and fitness-related traits using the Speckled Wood butterfly, *Pararge aegeria* (L.). Exposure to AcMNPV significantly reduced survival to pupation. For surviving larvae, sub-lethal infection significantly decreased daily mass acquisition rates and pupal mass. Growth on drought stressed plants increased daily mass acquisition rates resulting in heavier pupae, and increased resource allocation to adult reproduction. The interaction between host plant drought and viral exposure resulted in different resource allocation strategies, and thus different growth trajectories, between larvae. This in turn resulted in significantly different allometric relationships between larval mass (at inoculation) and both development time and investment in flight muscles. For larvae with relatively lighter masses there was a cost of resisting infection when growth occurred on drought stressed host plants, both within the larval stage (i.e. longer larval development times) and in the adult stage (i.e. lower investment in flight muscle mass). This multi-factor study highlights several potential mechanisms by which the complex interplay between low host plant nutritional quality due to drought, and pathogen exposure, may differentially influence the performance of *P. aegeria* individuals across multiple life stages.

1. Introduction

With global climate change emergent infectious diseases have risen significantly and climate warming has resulted in changes in the severity and prevalence of some infectious diseases, pests and pathogens (Daszak et al., 2000; Jones et al., 2008; Bebber, 2015; Shikano and Cory, 2015; Kolb et al., 2016; Ogden and Lindsay, 2016). In ectotherms, like herbivorous insects, climate change can impact host-pathogen dynamics both directly and indirectly. For example, rising temperatures can directly increase the likelihood of an insect herbivore encountering pathogens via increased feeding rates (Elder and Reilly, 2014). Increasing temperature and carbon dioxide levels may also reduce insect immune functioning and thereby directly increase susceptibility to disease by decreasing host plant quality (increasing plant defensive traits and decreasing nitrogen content) thereby decreasing immune functioning (Shikano and Cory, 2015). Another, as yet, underexplored mechanism by which climate change may impact host-pathogen dynamics is via an increase in the rate and magnitude of climatic extremes such as drought (e.g. Kolb et al., 2016). Similar to the indirect effects of increasing temperature on host plant quality, growth on drought-

stressed host plants also has the potential to decrease insect herbivore immune functioning via its negative effects on host plant quality. Host plant quality can indirectly affect insect-pathogen interactions via two main routes, altering the susceptibility of the insect to the pathogen, and/or changing the behaviour of the insect (Cory and Hoover, 2006; Shikano, 2017). For example, many phytochemicals, such as defensive allelochemicals, can modify the physiology and growth of insects by affecting their susceptibility to infection (Cory and Hoover, 2006; Shikano, 2017). Drought can induce changes in the chemical composition of plants, affecting the concentration and balance of nutrients, altering levels of defensive allelochemicals and/or changing levels of volatile stress metabolites (Mattson and Haack, 1987). Drought-induced chemical changes in plants can influence interactions between insects and their pathogens directly, or indirectly by enhancing the insect's immune system (Mattson and Haack, 1987). For example, high levels of allelochemicals in drought stressed plants consumed by insects can inhibit the growth of ingested pathogens (Mattson and Haack, 1987). Additionally drought-induced changes in nutrition can alter the insect's capacity to suppress pathogenic microorganisms (Mattson and Haack 1987).

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Effective resistance to pathogens is often dependent on resource availability and resource quality, because resource availability and quality improves body condition and also immune system deployment (Shikano and Cory, 2015; McKay et al., 2016). From ecoimmunological studies and life history theory, there is good evidence that investment in pathogen defences comes at the expense of other physiological processes such as growth and reproduction (Stearns, 1992; Ricklefs and Wikelski, 2002; Schmid-Hempel, 2005; McKay et al., 2016). These life history trade-offs may be exacerbated by development on low quality host plants, as immune response and compensatory growth in response to low resource quality both use energy reserves from the same resource pool (Shikano and Cory 2015; McKay et al., 2016). Food restriction during development can alter fitness and immunity across both juvenile and adult life stages (McKay et al., 2016). Poor developmental nutrition has been shown to impact many adult fitness traits such as size (e.g. Nylin and Gotthard, 1998; Gibbs et al., 2012), reproductive success (e.g. McGraw et al., 2007; Gibbs et al., 2012; Schwenke et al., 2016) and adult lifespan and adult phenoloxidase activity (McKay et al., 2016). To further complicate matters, however, compensatory growth responses are not always predictable and depend on various factors such as species (e.g. Hayward and Wang, 2001; Zhu et al., 2001; but see Karl et al., 2013), social environment (Maclean and Metcalfe, 2001; Metcalfe and Monaghan, 2001), and physiological factors such as internal state and age (e.g. Nieceza and Metcalfe, 1997). Mangel and Munch (2005) identified a range of possible compensatory responses such as; (i) faster than normal growth immediately following the end of the deprivation period, (ii) faster than normal growth at some time later (long term compensation) and (iii) faster than normal growth and overtaking control individuals that continue to grow normally. As such there is unlikely to be a simple easily predictable response, and just knowing that immune functioning increases with resource quality may not be sufficient to determine the response of different species, or even different individuals within a species, to the interacting effects of food quality and pathogen exposure (Shikano and Cory, 2015). As such there is a need for more complex, multi-factor, studies to examine the impact of ecologically relevant pathogen species on host survival and other fitness traits under poor nutritional growth conditions (Shikano and Cory, 2015).

Using the model pathogen, the baculovirus *Autographa californica multinucleocapsid nucleopolyhedrovirus* (AcMNPV), we examined the interactive effects of growth on drought stressed host plants and sub-lethal pathogen challenge on survival and fitness-related traits using the Speckled Wood butterfly, *Pararge aegeria* (L.). Baculoviruses are highly pathogenic obligate killers that infect the larval stage via ingestion of contaminated leaf material (Cory and Myers, 2003; Harrison and Hoover, 2012). AcMNPV has a broad host range, infecting at least 15 lepidopteran families (Cory and Myers, 2003; Shikano and Cory, 2015). Sub-lethal baculovirus infections have been shown to incur fitness costs to their hosts such as reduced pupal weight and prolonged larval development time (Milks et al., 1998; Shikano and Cory, 2015) and also by delaying the onset of egg laying (Shikano et al., 2016). Pathogens can directly affect insect wing development both positively (Ryabov et al., 2009) and negatively (Wülker, 1985; de Miranda and Genersch, 2010) and may also have indirect effects through resource trade-offs during development between immune defence and investment in flight morphological traits (Zuk and Stoehr, 2002). In Monarch butterflies, infection with pathogens can directly reduce flight ability, but this however, was not shown to be related to changes in wing morphological traits (Bradley and Altizer, 2005). Little is known about the effects of sub-lethal baculovirus infection on wing development and flight morphological traits. To date most studies have only crudely quantified effects by measuring wing deformities (e.g. Milks, 1997; but see Hesketh et al., 2012).

Pararge aegeria is one of the six most drought-sensitive butterfly species in the UK, whose populations could, under Global Climate Models of 'business-as-usual' emissions, suffer widespread extinctions

by 2050 (Oliver et al., 2015). This butterfly species has been extensively researched and used as a model system for studies of insect ecology and life history evolution (e.g. Aalberg Hangen and Gotthard, 2014), including single factor studies examining life history trade-offs in response to drought (Gibbs et al., 2012; Vande Velde et al., 2013) and viral infection with AcMNPV (Gibbs et al., 2010a; Hesketh et al., 2012). Little is known about the full range of pathogens *P. aegeria* encounter in nature, or the impact of known sub-lethal infections with bacteria (e.g. *Wolbachia*, Carter et al. 2013) or viruses (e.g. Rhabdoviruses, Longdon et al., 2017) on life history traits in natural populations. Previous laboratory studies on *P. aegeria* have shown that infection with AcMNPV reduces survival (Gibbs et al., 2010a; Hesketh et al., 2012), but has no observable sub-lethal direct effects on larval development time, pupal mass or adult wing morphology when larvae are growing under conditions of good resource availability and quality (Gibbs et al., 2010a; Hesketh et al., 2012). Drought stressed host plants have been shown to have reduced quality for *P. aegeria* larvae, with lower levels of foliar nitrogen, carbon and water available for consumption (Talloe et al., 2004), affecting adult mass, survival and investment in flight morphological traits (Talloe et al., 2004; Gibbs et al., 2012). *Pararge aegeria* is therefore an ideal model system with which to examine the impact of complex interactions between environmental factors on survival and fitness related traits.

2. Methods

2.1. Study species, *Pararge aegeria*

Along the pure capital breeding to pure income breeding continuum, *P. aegeria* sits closest to the capital breeding end of the spectrum and females of this species mostly rely on nitrogenous resources acquired during the larval stage for egg production (Bauerfiend and Fischer, 2008). There is little opportunity for females to obtain more nitrogenous resources for reproduction through adult feeding (Karlsson, 1994; Vande Velde and Van Dyck, 2013) or nuptial gifts (Svärd and Wiklund, 1989). During nectar and honeydew feeding, adults imbibe a dilute aqueous solution of mainly sugar with some lipids and minute quantities of amino acids (Jervis et al., 2008). Therefore, through adult feeding *P. aegeria* may gain extra carbohydrate and lipid resources to fuel somatic maintenance and flight (cf. Jervis et al., 2008; Vande Velde and Van Dyck, 2013). A sexual size dimorphism in size occurs in *P. aegeria* (Sibly et al., 1997), and selection for large female size (and hence high fecundity) appears to be more important for fitness than selection for large male size (Gotthard et al., 1994; Leimar et al., 1994).

2.2. Baculovirus production

A plaque-purified variant of AcMNPV designated C6 (Possee, 1986) was propagated in *Spodoptera frugiperdu cells* (IPLB-Sf-21) (Vaughn et al., 1977). A stock of AcMNPV was obtained as described in Gibbs et al. (2010a). In brief, a stock of AcMNPV was obtained by dosing 3rd instar *Trichoplusia ni* (Hübner) larvae. Viral inoculum was added to small plugs of artificial diet and larvae were maintained individually and allowed to feed overnight. Once the entire plug of diet was consumed, larvae were incubated in individual pots containing artificial diet until death due to virus. Viral cadavers were collected, macerated and the resulting suspensions filtered through sterile muslin to remove large particulate matter. Viral material was then purified using density gradient centrifugation. The concentration of occlusion bodies was estimated by counting three times in an improved Neubauer haemocytometer at magnification 400× (< 10% error in counts) (cf. Hesketh et al., 2012). Dilution of the stock suspension was done in sterile distilled water to achieve a final concentration of 1×10^6 OBs μl^{-1} for use in experiments. Previous studies (using the same methodology as described for this current study) with the model system, AcMNPV verified that when exposed to 1×10^6 OBs ml^{-1} at 21 days of larval

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