Drivers of aggregation in a novel arboreal parasite: the influence of host size and infra-populations

Kirsty J. Yule *, Kevin C. Burns

School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6012, New Zealand

ARTICLE INFO

ABSTRACT

As a novel arboreal parasite, New Zealand's largest endemic moth, *Aenetus virescens*, is a biological oddity. With arguably the most unusual lepidopteran life history on earth, larvae grow to 100 mm, spending ~6 years as wood-boring parasites feeding on host tree phloem. Parasite fitness is a product of host suitability. Parasite discrimination between heterogeneous hosts in fragmented populations shapes parasite aggregation. We investigated whether *A. virescens* aggregation among hosts occurs randomly (target area effect), or if larvae select hosts based on host quality (ideal free distribution). Using long-term larval growth as an indicator of energy intake, we examined *A. virescens* aggregation in relation to host size and infra-population. Using a generalised linear model, the relationship between parasite intensity and host tree size was analysed. Reduced major axis regression was used to evaluate *A. virescens* growth after 1 year. Linear mixed-effects models inferred the influence of parasite infra-population on parasite growth, with host tree as a random factor. Results indicate parasite intensity scaled positively with host size. Furthermore, parasite growth remained consistent throughout ontogeny regardless of host size or parasite infra-population. *Aenetus virescens* aggregation among hosts violates the ideal free distribution hypothesis, occurring instead as a result of host size, supporting the target area effect.

© 2014 Australian Society for Parasitology Inc. Published by Elsevier Ltd. All rights reserved.

1. Introduction

Host quality determines parasite growth, reproductive success, and survival (Théron et al., 1998; Poulin et al., 2003; Barber, 2005; Tschirren et al., 2007; Poulin and Forbes, 2011). Parasites aggregate, whereby few parasites infect many hosts and many parasites infect few hosts (Shaw et al., 1998; Tschirren et al., 2007; Calabrese et al., 2011; Poulin and Forbes, 2011; Poulin, 2013). Understanding parasite distribution patterns among hosts is crucial for accurate modelling of population dynamics (Poulin, 2000). Among hosts, exposure and susceptibility to parasites is heterogeneous, correlating with host size and age, driving parasite aggregation (Grutter and Poulin, 1998; Shaw et al., 1998; Poulin, 2013). Heterogeneity in host nutritional quality also influences parasite aggregation (Poulin et al., 2003; Tschirren et al., 2007). Endoparasites encounter finite resources (Poulin, 2007, 2013; Randhawa and Poulin, 2009; Daniels et al., 2013) and intensity-dependent resource competition reduces host quality, regulating parasite body size (Poulin, 1999; Barber, 2005). Furthermore, parasite dissemination and infection mode influence host selection (Lester, 2012; Poulin,

2013). Overall parasite success relies on discriminating between heterogeneous hosts in fragmented populations (Théron et al., 1998). Host selection is particularly significant for New Zealand's largest endemic moth, *Aenetus virescens* (Doubleday) (Lepidoptera: Hepialidae), which has arguably the most unique lepidopteran life history on earth.

Aenetus virescens is a biological oddity. Male moths attain a wingspan of 150 mm (Fig. 1A) (Grehan, 1981, 1984). In flight, female moths oviposit eggs onto forest floors where first larval instars are mycophagous (Grehan, 1981, 1984; Tobi et al., 1993). Subsequent larvae select, ascend and parasitise a host tree, excavating a "7"-shaped tunnel into tree heartwood. Larvae remain enclosed for ~6 years, growing to 100 mm (Fig. 1B), feeding on phloem tissue at the tunnel entrance (Grehan, 1981, 1983, 1984; Tobi et al., 1993). A feeding scar is created, surrounding the tunnel opening (Fig. 1C). Constructions of silk and frass webbing cover feeding scars, behind which larvae feed nocturnally (Grehan, 1984; Tobi et al., 1993). Webbing potentially conceals larvae from predatory North Island kaka, *Nestor meridionalis septentrionalis*, or from invertebrates such as tree weta, *Hemidenina* spp., that shelter in vacated tunnels. Larvae remain solitary and concealed throughout arboreal development, with no direct conspecific interaction until mating after emergence. Larvae pupate within the tunnel entrance, emerging as moths in summer with no functioning

---

* Corresponding author. Tel.: +64 (0)4 463 5233x8868.
  E-mail address: kirsty.yule@vuw.ac.nz (K.J. Yule).

mouth parts and survive only 1–2 days (Grehan, 1981). Despite this remarkable parasitic life history, the ecological role of *A. virescens*, in particular the relationship with host trees, is poorly understood.

Host trees parallel islands, comprising large, complex, ecological entities surrounded by uninhabitable space (Kuris et al., 1980; Southwood and Kennedy, 1983). The Ideal Free Distribution theory (IFD) predicts free and mobile organisms select habitat "islands" providing the greatest reward (Tregenza, 1995; Tyler and Gilliam, 1995; Stewart and Komers, 2012; Williams et al., 2013). Beneath tree outer bark, phloem carries photosynthates from the canopy to the roots (Högberg et al., 2001; Zwieniecki et al., 2004; Pompon et al., 2011). Phloem thickness scales strongly with tree diameter (Amman, 1969; Speights and Conway, 2010; Hölttä et al., 2013; Davis and Hofstetter, 2014), is a nutrient-rich resource (Pompon et al., 2011), and the sole foodstuff of *A. virescens*. Conversely, the hydrostatic conductance of phloem is reduced in older, larger trees, indicating a decreased flow of photosynthates (Yoder et al., 1994; Bond, 2000; Hölttä et al., 2013). Whilst larger trees present a greater quantity of food, nutritional quality is likely reduced. If *A. virescens* discriminate between hosts with varying nutritional benefits, smaller trees will have a greater parasite intensity. However, the Target Area Effect (TAE) states larger habitable "islands" merely represent larger targets more easily intercepted by randomly dispersing individuals (MacArthur and Wilson, 1967; Lomolino, 1990; Matter and Roland, 2003). For example, larger hosts present larger surface areas, and thus an increased chance of discovery by parasites (Poulin, 2013). Moreover, larger hosts tend to be older and have had longer to accrue parasites (Poulin, 2013). If *A. virescens* disperse randomly, larger trees will have greater parasite intensity than smaller trees.

Energy intake scales with body size and growth (see Lindstedt et al., 1986; Keeley and Grant, 1995; Greenleaf et al., 2007). When *A. virescens* feed, phloem tissue is masticated and the contents ingested. The resulting feeding scar is indicative of the phloem quantity consumed by an individual larva. If larvae can discern host quality, trees with greater available energy per unit of phloem will have greater parasite intensity. Moreover, parasites consuming equivalent phloem quantities should have increased growth rates in higher quality hosts (Barber, 2005; Tseng and Myers, 2014). Within an "island", however, available energy is a function of competitor intensity and discrete resources (Tregenza, 1995; Randhawa and Poulin, 2009; Tseng and Myers, 2014) with host saturation reducing host quality (Kaplan and Denno, 2007). Parasite intensity scales negatively with parasite growth when parasite-to-host body size ratio is high (Poulin, 1999; Barber, 2005; Lagrue and Poulin, 2008). Moreover, large parasite intensities over-burden host resources, negatively influencing parasite growth, population dynamics and genetics (Barber, 2005; Poulin, 2007; Neuhäuser et al., 2010; Blasco-Costa and Poulin, 2013). *Aenetus virescens* body size is relatively small compared with host trees, however feeding scars extensively wound phloem, remaining after parasites vacate the host. Phloem wounding compromises tree fitness and host quality. Feeding scars directly above a focal individual interrupt phloem from reaching that individual. Summation of all feeding scars per host (both past and present parasites) represents the accumulated interruption to phloem per host. Cumulative wounding from multiple feeding scars produces large-scale phloem disruption, reducing host quality. *Aenetus virescens* growth should thus experience intensity-dependent regulation.

Here, we investigate whether *A. virescens* aggregation among hosts occurs randomly (TAE) or if larvae select hosts based on reward (IFD). Using long-term larval growth as a measure of host quality, we examine how host size and parasite intensity drive *A. virescens* aggregation. We answer the following three questions. (i) Does parasite intensity scale positively with host size? (ii) Does parasite body size scale positively with feeding scar size? (iii) Is parasite growth intensity-dependent?

2. Materials and methods

2.1. Study site

Data were collected in Zealandia, a mainland island reserve at the southern tip of the North Island, New Zealand (41°28′S, 174°74′W). The climate is mild and temperate, with elevations ranging from 160 to 380 m above sea level (m.a.s.l.) (Blick et al., 2008). Primary forest was cleared for agriculture in the late 1800s (Blick et al., 2008; Burns et al., 2012; Burns, 2012) and Zealandia now comprises 225 ha of successional broadleaf-conifer forest enclosed by a mammal-resistant fence. Introduced mammalian predators were eradicated in 2000, aiding the re-introduction of native fauna and flora, in particular native birds (Burns, 2012). Dominant broadleaf evergreen trees such as *Coprosma* spp. (Rubiaceae), *Melicytus ramiflorus* (Violaceae), *Aristotelia serrata* (Elaeocarpaceae), *Pseudopanax arboreus* (Araliaceae), *Dysoxylum spectabile* (Meliaceae) and *Schefflera digitata* (Araliaceae) are common. The dense understorey comprises tree ferns, *Cyathea* spp. (Cyatheaceae), shrubs including *Brachyglottis repanda* (Asteraceae), *Geniostoma rupestre* var. *languifolium* (Loganiaceae), *Piper excelsum* (Piperaceae), and vines such as *Rhipogonum scandens* (Ripogonaceae).
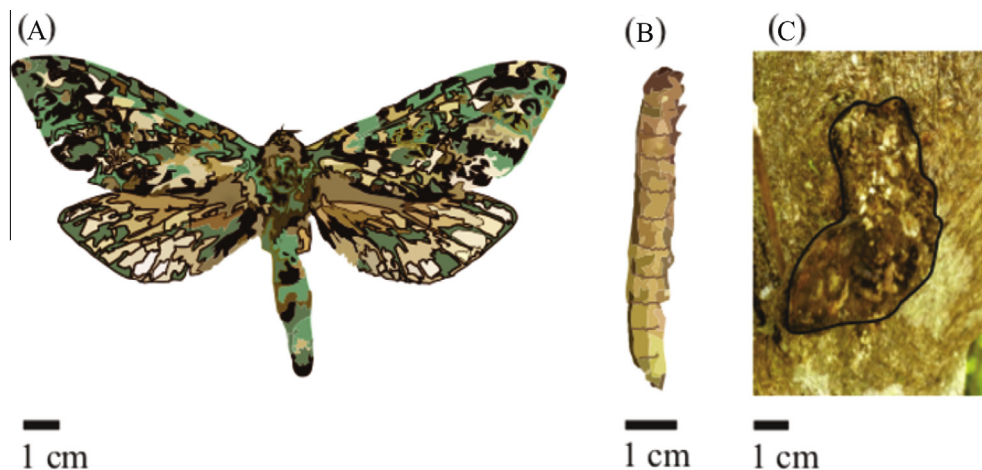

Fig. 1. New Zealand's largest endemic moth, *Aenetus virescens*. (A) Adult moth (female), (B) parasitic arboreal-phase larva, (C) parasite feeding scar on *Aristotelia serrata* host tree, covered with silk and frass webbing (webbing is outlined).