



# Reproductive characteristics of invasive hyperparasitoid *Baeoanusia albifunicle* have implications for the biological control of eucalypt pest *Paropsis charybdis*



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## HIGHLIGHTS

- Self-introduced hyperparasitoid thought to have reduced efficacy of control agent.
- Biological potential of *B. albifunicle* to disrupt *P. charybdis* control was assessed.
- *B. albifunicle* has a longer life, generation time and lower fecundity than its host.
- Hyperparasitism reduced successful primary parasitism to less than 10% in the lab.
- *N. insectifurax* is not hyperparasitised and might substitute for *E. nassau* decline.

## ARTICLE INFO

### Article history:

Received 8 June 2015

Revised 6 August 2015

Accepted 10 August 2015

Available online 10 August 2015

### Keywords:

Hyperparasitoid interactions

Encyrtidae

Pteromalidae

*Enoggera*

*Neopolycystus*

New Zealand

## ABSTRACT

Hyperparasitoids can impede the establishment of primary parasitoid biological control agents or limit their control capacity. Although modern quarantine practices generally prevent hyperparasitoids being introduced with biological control agents, introductions can occur via natural pathways or accidentally with incoming passengers and cargo. In New Zealand, *Baeoanusia albifunicle* Girault is a self-introduced hyperparasitoid of *Enoggera nassau* Girault, an intentionally introduced control agent of the eucalypt pest *Paropsis charybdis* Stål. A self-introduced primary parasitoid, *Neopolycystus insectifurax* (Girault), also parasitises *P. charybdis* in New Zealand. We assessed *B. albifunicle* biology to better understand its potential to disrupt *P. charybdis* control. It was determined that *B. albifunicle* is an obligate solitary hyperparasitoid with a longer lifespan, lower fecundity and longer generation time than its host. The hyperparasitoid reduced effective parasitism by *E. nassau* to <10% in the lab, indicating it may limit control of the first *P. charybdis* generation by slowing spring population growth. It was confirmed that *N. insectifurax* is not hyperparasitised by *B. albifunicle* and therefore has some potential to substitute for any hyperparasitoid-driven decline in *E. nassau*.

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## 1. Introduction

Internationally, records of deliberately or accidentally introduced hyperparasitoids are limited (e.g., Charles, 1993; Day, 2002; Gaines and Kok, 1999; Peck et al., 2008; Wang and Messing, 2004). However, considering the numerous examples of accidentally introduced pest insects, and a small but relevant number of primary parasitoids (e.g., Bjørnson, 2008; Calcatera et al.,

2007; Charles, 1993; Johnson et al., 2001; Peck et al., 2008), it is likely that hyperparasitoid incursions occur at higher frequencies than reported. While herbivore incursions and their damage may be conspicuous, the arrival of minute parasitoids is likely to go unnoticed unless they occur in intensively managed systems, yet their presence could have important consequences.

Obligate hyperparasitoids are generally considered integral in the regulation of primary parasitoids in their native range and detrimental to their use as biological control agents (BCAs) elsewhere (Rosenheim, 1998). Hyperparasitoids can jeopardise BCA establishment by limiting population growth before (Bain and Kay, 1989) or after (Gaines and Kok, 1999) release, or prevent established agents from attaining densities sufficient to suppress

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their hosts (Höller et al., 1993; May and Hassell, 1981; Rosenheim, 1998; Sullivan and Völkl, 1999). Consequently, screening to exclude hyperparasitoids from introduction with primary parasitoid BCAs has become a standard component of classical biological control in New Zealand and other countries with 'risk adverse' biosecurity policies. When selecting BCAs it is now also common to consider hyperparasitoid associations in the agent's native range and potential susceptibility to hyperparasitoids already present in the receiving country (Berry and Mansfield, 2006).

Basic invasion theory predicts ample opportunity for natural and accidental introductions of Australian insects to New Zealand as a result of geography, wind patterns, high volume trade and travel (Close et al., 1978; Fox, 1973; Ridley et al., 2000). Incursions of specialist eucalypt herbivores occur with particularly high frequency and several Australian parasitoids have been imported to New Zealand to control these pests in exotic eucalypt plantations (Withers, 2001). In addition to intentional introductions, at least five primary parasitoids of introduced eucalypt psyllids and one of paropsine beetles have been detected since the 1860s. Two hyperparasitoids also appear to have established without intentional human assistance (Berry, 2006): *Coccidoctonus psyllae* Riek (Hymenoptera: Encyrtidae) attacking the psyllid parasitoid *Psyllaephagus* sp. (Encyrtidae), and *Baeoanusia albifunicle* Girault (Encyrtidae) attacking *Enoggera nassau* Girault (Hymenoptera: Pteromalidae), the primary parasitoid BCA of *Paropsis charybdis* Stål (see below). As parasitoid BCAs introduced from Australia to New Zealand may associate with several hosts or share host species with other parasitoid species in Australia, the high rate of trans-Tasman dispersal could result in BCAs encountering new hosts, competitors, or natural enemies from their native range that were absent when they were initially introduced.

In New Zealand, four species of Australian paropsine beetles (Chrysomelidae: Paropsini) are established and others have been intercepted at the border or eradicated (Withers, 2001; Bain, 2013). In Australia these defoliators are regulated by a range of dipteran and hymenopteran primary parasitoids, themselves regulated by a suite of hyperparasitoids (de Little, 1982; Greaves, 1966; Tribe, 2000). In New Zealand, *P. charybdis* initially constrained the establishment of a commercial eucalypt industry and remains the most serious eucalypt plantation defoliator today (New Zealand Forest Service, 1976; Withers, 2001). Early attempts at biological control failed, often because imported agents arrived heavily hyperparasitised by their Australian natural enemies (Bain and Kay, 1989). Control was eventually achieved following the introduction of the solitary egg parasitoid, *E. nassau*, from Western Australia in 1987 (Kay, 1990). However, recent self-introductions of *Neopolycystus insectifurax* (Girault) (Pteromalidae) (Berry, 2003), a solitary primary egg parasitoid that competes directly with *E. nassau* for hosts, and the solitary hyperparasitoid *B. albifunicle* (Jones and Withers, 2003) are thought to have altered these control dynamics.

The biology and behaviour of *E. nassau* and *N. insectifurax* are compared elsewhere (Mansfield et al., 2011; Murray et al., 2009). Interactions between them have not been assessed in the absence of *B. albifunicle* in Australia and the biology of *B. albifunicle* itself has received little attention. Tribe (2000) noted large head and mandibles of larvae, a female-biased sex ratio, and concluded *B. albifunicle* was an obligate hyperparasitoid, but experiments were limited in replication and host eggs were presented to both primary and secondary parasitoids simultaneously. Field monitoring in New Zealand has shown *E. nassau* is heavily hyperparasitised by *B. albifunicle*, leading to speculation that *P. charybdis* control has been disrupted (Berry and Mansfield, 2006; Jones and Withers, 2003; Murray et al., 2008). As there is no evidence that *N. insectifurax* is also hyperparasitised, it could potentially complement or substitute for control provided by *E. nassau*. Here, we

investigate the biological characteristics of *B. albifunicle* to assess its potential to disrupt the previously well-established biological control of *P. charybdis*.

## 2. Materials and methods

### 2.1. Insect cultures

All insect colonies were maintained at  $22 \pm 2$  °C, 65% r.h., and L14:D10. *P. charybdis* were reared in ventilated perspex cages (1.0 m × 0.7 m × 0.7 m). Fresh cut field-grown *Eucalyptus nitens* (Deane et Maiden) Maiden flush foliage was provided as food. Egg batches laid on the foliage were collected every 2–3 days and stored at 4 °C for up to five days. Individual *E. nassau* and *N. insectifurax* females  $\geq 3$ -days-old were presented with these egg batches for 24 h in 90 mm Petri dishes in a separate room. Parasitised batches were maintained in Petri dishes in groups of five until emergence. Progeny were supplied undiluted honey on 20 mm<sup>2</sup> paper-towel, and left to mate in the presence of the natal host eggshell.

*B. albifunicle* were maintained in 65 mm Petri dishes in a controlled climate cabinet (Custom made, Scion). *P. charybdis* egg batches, parasitised by *E. nassau* over the preceding 24 h, were presented to groups of five 3–5 day-old *B. albifunicle* females (sexed using antennae morphology: female flagellum clubbed, male plumose) for 48 h. *E. nassau* that escaped hyperparasitism were removed at emergence nine days later. Hyperparasitoids emerged after 14 days and were provided undiluted honey as above.

Experiments were conducted in growth cabinets (22 °C, 65–70% r.h., L14:D10) in which all egg batches exposed to parasitoids were subsequently held for up to 21 days to record their fate. As neither *E. nassau* nor *N. insectifurax* are sexually dimorphic it was not possible to expose the desired number of hosts to female parasitoids in every experiment. Generally, behavioural observation at the beginning of each experiment verified the wasps used were in fact female. However, all parasitoids were dissected after experiments to confirm their sex and hosts exposed to males were discarded as replicates.

### 2.2. Obligate or facultative hyperparasitism

Tribe (2000) reported *B. albifunicle* to be an obligate hyperparasitoid following exposure of paropsine eggs to *B. albifunicle* either without or simultaneously with a primary parasitoid. Murphy (2002) described *B. albifunicle* as ovipositing into unparasitised *P. charybdis* eggs and developing only if the host was subsequently parasitised by a primary parasitoid. If *B. albifunicle* is an obligate hyperparasitoid the latter strategy could provide opportunity for it to evolve facultative hyperparasitism. The following trials were conducted to confirm if *B. albifunicle* is an obligate hyperparasitoid and when it must oviposit relative to its primary parasitoid host. In trial one, *P. charybdis* egg batches were placed in separate Petri dishes, provisioned with honey, and exposed to individual 3-day-old females of either *B. albifunicle* or *E. nassau* for 24 h ( $n = 20$  per species). Half ( $n = 10$ ) the batches exposed to each species were then immediately presented to the other species for a further 24 h. In trial two, egg batches were exposed to *E. nassau* (2 h) followed by *B. albifunicle* for a further 2 h after an interval of 2, 4, 6, 12 or 24 h since the start of the first exposure period ( $n = 10$  per time interval). For trial one and two the number of *P. charybdis*, *E. nassau* and *B. albifunicle* that later emerged was recorded. Trial three followed the procedures of trial two but with exposure to *B. albifunicle* after intervals of 30, 1, 24, 12, 18, 15, 17 and 16 h ( $n = 20$  per interval). As appropriately aged insects were

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