

Response of parasitoid egg load to host dynamics and implications for egg load evolution

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Keywords:

Braconidae;
Euphorinae;
fecundity;
host synchrony;
Microctonus hyperodae;
oviposition rate;
proovigeny;
resource allocation;
adaptive asynchrony;
trade-off.

Abstract

A theoretical debate about whether parasitoids should be time or egg limited now recognizes both as feasible, and interest has turned to determining the circumstances under which each might arise in the field, and their implications for parasitoid behaviour and evolution. Egg loads of parasitoids sampled from the field are predicted to show a negative response to host availability, but empirical support for this relationship is scarce. We measured how a parasitoid's egg load responded to seasonal fluctuations in host population density and recorded the predicted correlation. In early summer, parasitoids were at high risk of time limitation due to low host availability, and in late summer, their offspring were at greater risk of egg limitation due to high host availability. Despite clear seasonal changes in selection pressures on egg load and lifespan, the parasitoid showed no evidence of seasonal variation in its reproductive strategy. We made minor modifications to a previously published model to explore the effects of seasonal variation in host availability on optimal investments in eggs and lifespan and obtained several new results. In particular, under circumstances analogous to some of those observed in our field study, temporal stochasticity in reproductive opportunities can cause investments in eggs to increase, rather than decrease as previously predicted. Our model results helped to explain the parasitoid's lack of a seasonally varying reproductive strategy. Understanding the evolution of parasitoid egg load would benefit from a shift of research emphasis from purely stochastic variation in parasitoid reproductive opportunities to greater consideration of host dynamics.

Introduction

The total number of eggs produced by female parasitoids should be selected to match the number of host insects they encounter, but environmental stochasticity thwarts perfect matches (Rosenheim, 1996). Thus, females may die before exhausting their eggs (time limitation) or exhaust their eggs before dying (egg limitation). In general, parasitoids' egg supplies should increase with the mean and variance of their realized fecundity (Godfray, 1994), which will vary spatially and temporally (Godfray *et al.*, 1994; van Nouhuys & Lei, 2004; Stireman *et al.*, 2005; Forkner *et al.*, 2008).

Rosenheim (2011) summarized how models of parasitoid reproductive behaviour and parasitoid–host population dynamics have produced differing predictions depending on whether they emphasized egg or time limitation, and reviewed the resulting debate about the relative contributions of eggs and time to oviposition costs. Rosenheim (1996, 1999, 2000) advocated that a proportion of parasitoids must become egg limited for a balance between eggs and lifespan to evolve, whereas Sevenster *et al.* (1998) and Eilers *et al.* (2000) argued that spatial stochasticity in reproductive opportunity increased investment in eggs and reduced egg limitation to negligible levels.

Rosenheim (2011) evaluated these differing perspectives by developing a model that optimized lifetime reproductive success under either spatial or temporal stochasticity by trading off resource allocations between eggs and lifespan, while assuming a range of values for

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egg cost. Stochasticity in reproductive opportunity was simulated using a probabilistic survival function to incorporate variation in parasitoid lifespan (which is mathematically identical to a model that incorporates variation in host encounter rates), while assuming a constant oviposition rate (Rosenheim, 2011). Consistent with earlier results (Sevenster *et al.*, 1998; Ellers *et al.*, 2000), spatial stochasticity favoured increased egg loads, but was countered by temporal stochasticity, which caused egg loads to decline whenever egg costs were moderate to high. This arose due to the fitness penalty imposed by temporal heterogeneity, but not spatial heterogeneity, on high egg loads and short lifespans during generations when reproductive opportunities were scarce and extinction risks were high (Rosenheim, 2011). However, both spatial and temporal stochasticity increased the evolutionary significance of egg limitation because, in variable environments, only a small proportion of females achieved high fecundity, and this minority of predominantly egg limited parasitoids produced most of the total population's offspring (Rosenheim, 2011).

Most models of egg load evolution have assumed purely stochastic variation in parasitoid reproductive opportunity, although Van Baalen (2000) and Gandon *et al.* (2009) recognized that parasitoid egg load evolution should also be strongly influenced by host population dynamics. Using an epidemiological model in which parasitoid reproduction responded to host population size, Gandon *et al.* (2009) recovered a result obtained from stochastic models that egg load should increase with oviposition rate.

Empirical support for the prediction that low rates of egg limitation should be common in nature (Heimpel & Rosenheim, 1998; Casas *et al.*, 2000; Rosenheim, 2011; Segoli & Rosenheim, 2013) has proved elusive (Rosenheim *et al.*, 2008), and even the expected negative relationship between parasitoid egg load and host population size (Rosenheim, 1996; Mangel & Heimpel, 1998; Sevenster *et al.*, 1998; Ellers *et al.*, 2000; Gandon *et al.*, 2009) has seldom been recorded (Phillips *et al.*, 1998; Dieckhoff *et al.*, 2014). It is difficult to use egg counts obtained by dissecting females sampled in the field to estimate egg limitation rates because many parasitoid species exhibit adaptations for adjusting their investments in time and eggs in response to environmental cues (Rosenheim *et al.*, 2008). Adaptations that reduce risks of egg limitation include the ability to vary egg production rates (Papaj, 2000; Casas *et al.*, 2009; Dieckhoff *et al.*, 2014); vary oviposition rates (Casas *et al.*, 2000); accept or reject hosts for oviposition, superparasitize hosts and adjust clutch size (Mangel & Heimpel, 1998; Papaj, 2000; Rosenheim *et al.*, 2008); resorb eggs (Rosenheim, 2000; Richard & Casas, 2009); and extend lifespan through feeding (Richard & Casas, 2009). An additional impediment to estimating egg limitation risks is inadequate knowledge of parasitoid age distributions and oviposition rates (Rosenheim, 1999).

Synovigenic parasitoids mature new eggs throughout their lifetimes and may possess all or many of the previously noted adaptations for adjusting their investments in time and eggs. In contrast, proovigenic parasitoids' investments in eggs are fixed upon emergence, and they are unable to vary egg production rates or resorb eggs. Proovigenic species are also less able to adjust their investments in time because, unlike many synovigenic species, they do not host feed (Jervis *et al.*, 1996). Thus, proovigenic species have advantages over synovigenic species for studying egg limitation.

This article describes a 4-year field study of interactions between the egg loads of a proovigenic parasitoid and the dynamics of its host population. We observe features of their interactions that are inconsistent with assumptions common to many previously published models of parasitoid egg load evolution. Thus, we explore the implications of our field observations for parasitoid egg load evolution by making minor modifications to Rosenheim's (2011) model. Our field data and simple model modifications produce new insights and show that careful consideration of host dynamics is critical to understanding parasitoid egg load evolution.

Materials and methods

Model system

The host insect is the adult stage of *Listronotus bonariensis* (Kuschel) (Coleoptera: Curculionidae), which is a South American weevil, first recorded in New Zealand in 1927, that feeds on grasses (Goldson *et al.*, 1998a). *Listronotus bonariensis* overwinters in the adult stage. After winter, population densities of adults decline and reach a minimum of nearly zero about mid-December (early summer), then rapidly increase with the emergence of new generation adults (Goldson *et al.*, 1998a). Population densities of adults peak either during the first generation in mid-to-late January, or during a second generation in March to April (Goldson *et al.*, 1998a). Over 5 years, minimum adult densities in mid-December (early summer) were always $< 8 \text{ m}^{-2}$, whereas peak adult densities in January to April (summer to autumn) ranged from 131 to 436 m^{-2} (Goldson *et al.*, 1998a).

The endoparasitoid, *Microctonus hyperodae* Loan (Hymenoptera: Braconidae, Euphorinae), was introduced from South America to New Zealand in 1991 for biological control of *L. bonariensis*, where it is now widely established (Phillips *et al.*, 2008). *Microctonus hyperodae* has no other hosts (Loan & Lloyd, 1974; Barratt *et al.*, 1997), nor any specialist natural enemies in New Zealand. It overwinters in adult hosts as a first instar larva, which emerges in spring to pupate in the soil (Goldson *et al.*, 1998b). A phenological model (Barlow *et al.*, 1994) and field observations (Goldson *et al.*, 1998b) indicate there is a period of low host availability

during December (early summer) due to *M. hyperodae* adults emerging before *L. bonariensis* adults. Up to two further parasitoid generations occur before winter (Barlow *et al.*, 1994; Goldson *et al.*, 1998b) and these coincide with much higher host densities (Goldson *et al.*, 1998a).

Microctonus hyperodae reproduces by thelytoky (i.e. unfertilized females have female offspring; Loan & Lloyd, 1974; Iline & Phillips, 2004). Oogenesis occurs before and immediately after eclosion of the adult, no further eggs are produced during the parasitoid's lifetime, and the eggs cannot be resorbed (Goldson *et al.*, 1995; Phillips & Baird, 2001). This reproductive strategy is effectively proovigenic (Shaw & Huddleston, 1991) because the egg storage capacity of the parasitoid equals its maximum potential lifetime reproductive success (Heimpel & Rosenheim, 1998), although it has been more strictly defined by Jervis *et al.* (2001) as synovigenic because maturation of some eggs occurs immediately after adult eclosion (C.B. Phillips, unpublished data). *Microctonus hyperodae* adults do not host feed (Phillips, 2002), which is a behaviour absent from all proovigenic parasitoids (Jervis *et al.*, 1996). Laboratory experiments have demonstrated that feeding on floral nectar can extend the longevity of *M. hyperodae* adults from about 8 days to about 21 days (Vattala *et al.*, 2006). However, measurements of sugar concentrations in field-collected *M. hyperodae* females indicate that few feed in New Zealand grassland because suitable nectar sources are scarce (Vattala, 2005; C.B. Phillips, unpublished data). Therefore, *M. hyperodae* is an excellent model for studying parasitoid egg limitation due to its relatively restricted capacity to adjust its investments in time and eggs.

Microctonus hyperodae deposits a single egg in the haemocoel of the adult weevil, and a solitary larva develops within the living host. There is no evidence that *M. hyperodae* responds to variation in host quality (Urrutia *et al.*, 2007) except that oviposition in already-parasitized hosts is usually avoided (McNeill *et al.*, 1996). In occasional cases of superparasitism (McNeill *et al.*, 1996), only one larva completes its development.

The mean pre-oviposition egg load of *M. hyperodae* shows a weak positive response to temperature. Parasitoids reared in the laboratory at 20 °C had a mean pre-oviposition egg load of 47 ± 14 (± 1 SD) eggs (Phillips & Baird, 2001; Urrutia *et al.*, 2007), whereas those reared at 15 or 25 °C had means of 43 ± 8 and 50 ± 7 eggs, respectively (C.B. Phillips, unpublished data). *Microctonus hyperodae* reared in the laboratory also shows a weak positive relationship between pre-oviposition egg load and body size (Phillips & Baird, 2001; Urrutia *et al.*, 2007). Smaller females with a hind tibia length of 600 μm had a mean pre-oviposition egg load of 38 eggs, and larger females with a hind tibia length of 850 μm had 55 eggs (Phillips & Baird, 2001; Urrutia *et al.*, 2007). However, pre-oviposition egg load of

laboratory-reared *M. hyperodae* varies neither with host diet (Urrutia *et al.*, 2007), parasitoid age (Phillips & Baird, 2001) nor time of year (Phillips & Baird, 2001; Urrutia *et al.*, 2007).

Both *L. bonariensis* and *M. hyperodae* are abundant throughout New Zealand (e.g. Phillips *et al.*, 2008) where their main habitat, grassland, covers half of the country's land area (Anonymous 2010).

Sampling

Sampling was conducted in one ryegrass/white clover field (100 m x 100 m) at Lincoln, Canterbury, New Zealand, between September 1996 and August 2000. This was the same field used previously to describe the bionomics of *L. bonariensis* (Goldson *et al.*, 1998a) and *M. hyperodae* (Goldson *et al.*, 1998b) and to investigate the effects of providing floral nectar to *M. hyperodae* (Vattala, 2005).

Field densities of *L. bonariensis* adults were measured using the procedures of Goldson *et al.* (1998a). A flotation method (Proffitt *et al.*, 1993) was used to extract adult weevils from turf samples (450 mm x 40 mm x 80 mm deep) collected approximately fortnightly from 2 September 1996 to 2 March 1998. The pasture at the study site was renovated in March 1998, sampling was resumed on 8 September 1998 and was thereafter conducted at approximately six-weekly intervals until 22 August 2000. Parasitism rates were estimated by dissecting weevils under a stereo microscope to detect parasitoid eggs and larvae. Field densities of parasitoid eggs and larvae were calculated as the proportion of dissected hosts parasitized multiplied by the field density of hosts.

Adults of *M. hyperodae* were sampled each week by vacuuming leaf litter from up to four transects of pasture, each approximately 100 m long, using a modified leaf blower with an intake pipe of 150 mm diameter. *Microctonus hyperodae* adults were retrieved from the leaf blower samples and stored at 4 °C pending measurement of their egg loads. Field densities of adult parasitoids cannot be reliably estimated from this sampling method. Sampling was always conducted during daylight, usually between midday and 15:00 h. Most *M. hyperodae* oviposition occurs between dusk and dawn (Armstrong *et al.*, 1996), thus *M. hyperodae* egg loads were unlikely to substantively decline during daylight hours.

Parasitoid measurements

Each parasitoid's egg load was measured following Phillips & Baird (2001) by removing its ovaries, immersing them in a protein stain (0.1 g nigrosin (BDH) in 100 mL H₂O followed by 3 g trichloroacetic acid), then separating the eggs and counting them at approximately 100 \times magnification. The stain helped to

separate and colour the eggs, making them easier to count. To evaluate whether egg load varied with body size, the parasitoids' hind tibiae were measured using a stereo microscope fitted with an eyepiece micrometre.

Statistical analyses

Statistical analyses were conducted using Genstat v.6.1 (Genstat Committee, 2002). The independence of successive samples of parasitoid egg loads and host densities was tested by analysing sample autocorrelations within each of these time series. Variation in parasitoid egg load attributable to parasitoid generation, adult weevil density, time of year and year was examined using a generalized linear model with a Poisson error distribution for count data and a log link between the counts and the variables (McCullagh & Nelder, 1983). The relationship between parasitoid body size and egg load was examined the same way in a separate model. The procedures used each week to obtain adults of *M. hyperodae* and *L. bonariensis* differed and were not always performed on the same day. To examine the relationship between parasitoid egg load and *L. bonariensis* adult population density, linear interpolation was used to estimate weevil adult densities for the days on which parasitoid egg loads, but not weevil adult densities, had been measured. Probabilities were calculated using an approximate *F*-test based on ratios of mean deviances (McCullagh & Nelder, 1983).

Modification of Rosenheim (2011) model

We coded the egg load evolution model of Rosenheim (2011) in R (R Core Team 2012). It simulates stochasticity in reproductive opportunity using a Weibull function to incorporate variation in parasitoid lifespan (which is mathematically equivalent to variation in host encounter rate), while assuming a constant oviposition rate. Parasitoids trade off resource allocations to eggs or lifespan to optimize fitness under either temporal or spatial stochasticity. Readers are referred to Rosenheim (2011) for a full description of the model; here, we only describe our modification.

The original model assumed a constant oviposition rate, which we modified to vary linearly with parasitoid age; we inferred their slopes from our field data as described in the next section. Our minimum and maximum rates bounded the constant rate of 1 egg per hour used by Rosenheim (2011), which facilitated comparison between results from the original and modified models. Rosenheim (2011) defined parasitoid investment in reproduction, R , the cost of maturing one egg, s , and a constant oviposition rate, k , which gave each parasitoid a total of R/s eggs. To lay all of her eggs, a female must live to age $x = kR/s$, and a female that dies before laying all of her eggs has a lifetime reproduction of kx (Rosenheim, 2011). We substituted the constant k

with the equation for a straight line $k = ax + b$ and used integration to calculate parasitoid lifetime reproduction and the age when parasitoid egg supplies became exhausted. In the field study, we observed delays between parasitoid emergence and the start of oviposition. To model such delays, we used $b < 0$ and $a > 0$ and calculated the integral only for the positive portion of the line when $k > 0$. All other parts of Rosenheim's (2011) model including stochasticity in parasitoid lifespan and host availability were left unaltered. With our modification, parasitoids always experienced heterogeneity in reproductive opportunities, but exploited these opportunities either at an increasing or decreasing rate to approximate the seasonal fluctuations in host densities that we observed in the field. Rosenheim's (2011) model investigated the effects of both spatial and temporal stochasticity on optimal egg loads, but we only analysed the effects of temporal stochasticity because we were interested in how temporal changes in oviposition rate should influence egg load evolution.

Parasitoid oviposition rate estimates for modelling

Our field measurements of *M. hyperodae* egg loads strongly suggested that its oviposition rates were positively correlated with *L. bonariensis* adult densities, so we estimated biologically feasible values for a (oviposition rate) from the slopes of increasing or decreasing seasonal changes in densities of unparasitized *L. bonariensis* adults. Oviposition rates will likely also have been influenced by fluctuations in adult parasitoid density, which we were unable to measure. Thus, we do not propose these as accurate estimates. However, our conclusions are dependent on the signs and relative magnitudes of the slopes, which could be confidently inferred, rather than on their absolute values.

For the period within each season when host density markedly increased (see Results), a was calculated as the maximum density of unparasitized *L. bonariensis* adults minus the minimum density, divided by the intervening interval in hours. Thus, in the modified model, the linearly increasing oviposition rate increased from zero to 2 eggs per hour before becoming constant, which reflects the observation that parasitoid oviposition rates generally increase asymptotically with increasing host availability (Bernstein, 2000; Fernández-Arhex & Corley, 2003).

For the period within each season when host density markedly decreased (see Results), the negative slope was calculated in a similar way to the positive slope. It was measured from the summer peak density of unparasitized hosts to when the last *M. hyperodae* females were sampled at the end of each season. Thus, in the modified model, oviposition rates declined from 2 to 0.05 eggs per hour; this minimum approximated our field results, which showed that host densities declined to low levels then persisted.

Results

Autocorrelations

There were no significant correlations between successive measurements of parasitoid egg loads ($P > 0.05$). For successive measurements of host density, there were significant correlations at weeks one and two ($P < 0.05$), but no significant correlations in the remaining 28 weeks. Thus, we considered the assumption of linear regression that residuals are independent had been substantively met.

Population densities of parasitized and unparasitized *Listronotus bonariensis*

Figure 1 shows the total number of *L. bonariensis* adults per m^2 obtained by our sampling and the subset of weevils that contained a *M. hyperodae* egg or larva. The observed seasonal fluctuations in densities of parasitized and unparasitized weevils were consistent with those recorded by Goldson *et al.* (1998b). After September

(early spring), there was a marked decline in densities of parasitized and unparasitized weevils due both to parasitoid larval emergence and to normal mortality of an aged population of adult weevils that had persisted through winter. Maximum numbers of parasitized weevils corresponded with the times when weevil densities peaked, either during the first weevil generation in mid-to-late January, or during a second weevil generation in March to April (Fig. 1).

Temporal occurrence of adult parasitoids

Figure 2 shows the egg load of every parasitoid sampled by collection date, the mean egg load measured on each collection date and the number of unparasitized *L. bonariensis* per m^2 . A total of 441 *M. hyperodae* adults were obtained from collections made each week from the start of November until the end of May during 1996 to 2000. The first date adult parasitoids appeared in leaf blower collections was relatively consistent across years, whereas the last date varied widely. The first and last dates for each period were 18 November

Fig. 1 Total adult *Listronotus bonariensis* m^{-2} and parasitized adult *L. bonariensis* m^{-2} measured from September 1996 to June 2000. Error bars show 95% CI.

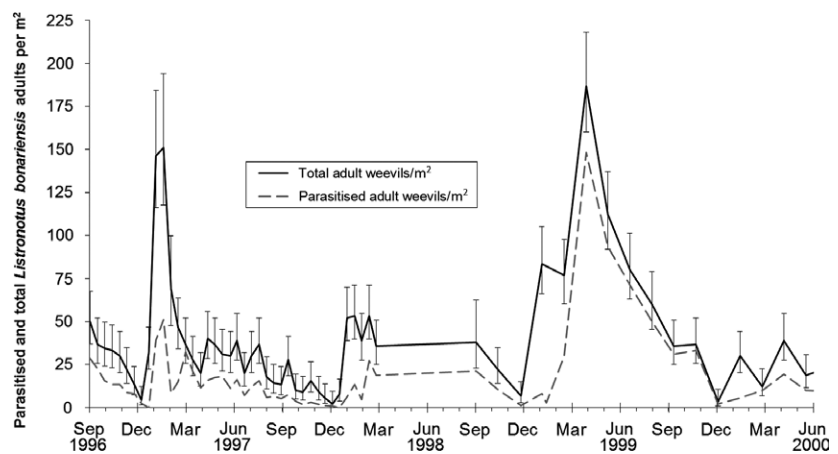
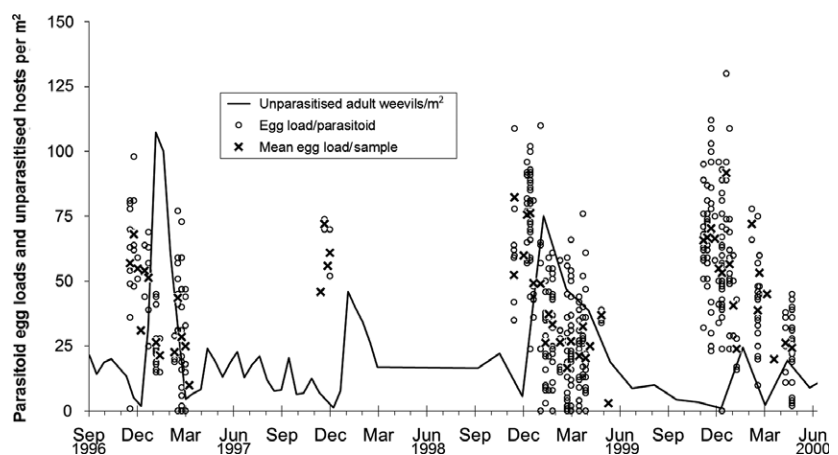


Fig. 2 Egg load per *Microctonus hyperodae*, mean egg load per sample and unparasitized *L. bonariensis* adults m^{-2} from September 1996 to June 2000.



1996–10 March 1997, 14 November 1997–2 December 1997, 16 November 1998–14 May 1999 and 10 November 1999–26 April 2000 (Fig. 2). At least one adult parasitoid was obtained in each weekly collection made between these dates, except on 18 November 1997 and on 16 January 1999 when no parasitoids were recovered. Of the 53 collections from which at least one adult parasitoid was sampled, a mean (\pm SE) of 8.3 ± 1.0 individuals per collection was obtained (range 1–28). The first *M. hyperodae* females emerged in November well before the weevil population began increasing in December due to the emergence of the first summer generation of adult weevils (Fig. 2).

Egg loads of adult parasitoids

Figure 3 shows the significant negative correlation between parasitoid egg load and host population density ($P < 0.001$), which was described by the curve $p = e^{4.13 - 0.0073d}$, where $d = \text{hosts m}^{-2}$. This relationship

was tested at high host densities by measuring regression residual deviance while truncating the host population density data to values ranging from 200 to 30 m^{-2} , using decrements of 1 m^{-2} . Minimum residual deviance occurred at 90 hosts m^{-2} , and there was no significant relationship with parasitoid egg load at higher host densities (Fig. 3). For host densities less than 90 m^{-2} , the relationship with parasitoid egg load was described by the curve, $p = e^{4.22 - 0.01095d}$, where $d = \text{hosts m}^{-2}$ ($P < 0.001$; Fig. 3). When host densities were at a mean annual minimum of 4 m^{-2} in the first week of December (Fig. 1), parasitoids contained a mean of 65 eggs, but when the first summer generation of hosts reached a mean annual peak of 96 m^{-2} in mid-January (Fig. 1), parasitoids contained a mean of 26 eggs (Fig. 3). The differing egg load distributions of parasitoids collected during November–December (spring–early summer) when hosts were scarce compared to those collected during January–May (mid-summer–autumn) when host were abundant are shown in Fig. 4

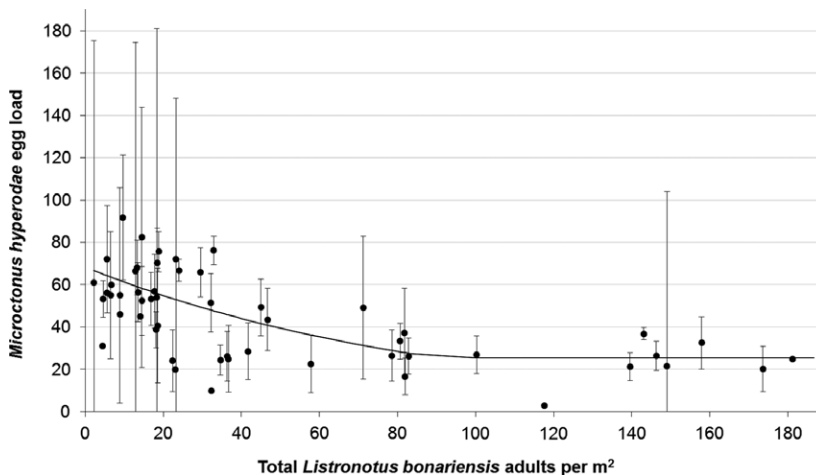


Fig. 3 Regression of *Microctonus hyperodae* egg load with *Listronotus bonariensis* adults m^{-2} . Points show mean egg load per sample with 95% CI.

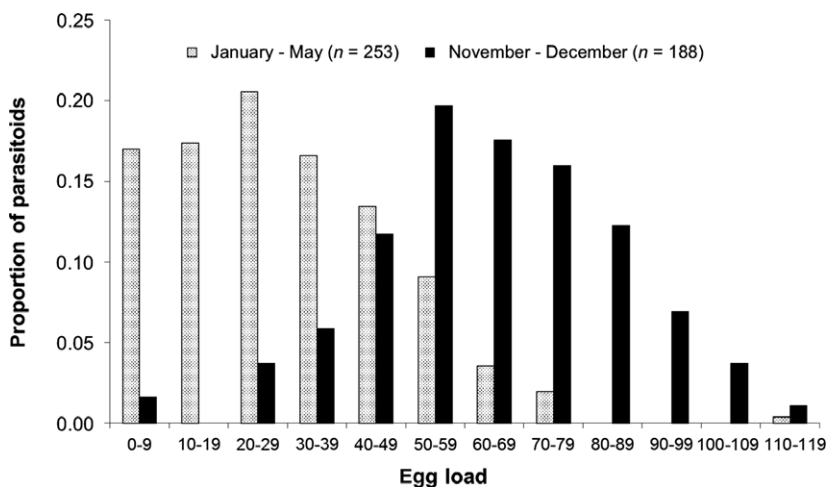


Fig. 4 Egg load frequencies of *Microctonus hyperodae* collected in early summer (November to December) and from mid-summer to autumn (January to May).

(chi-square test, d.f. = 9, Pearson $\chi^2 = 203.5$, expected value = 9, $P \ll 0.001$). Of the 441 females sampled, 15 (3%) had zero eggs. Irrespective of time of year, mean egg loads per sample (Fig. 1) sometimes exceeded the mean pre-oviposition egg load of about 47 eggs measured in laboratory studies (Phillips & Baird, 2001; Urrutia *et al.*, 2007); reasons for this apparent variation are currently unknown.

Body size was measured for a subsample of 79 parasitoids collected between November 1996 and March 1997. Body size was greatest at the start of the season and declined as the summer progressed ($P < 0.001$). Parasitoids collected in November had a mean (± 1 SD) hind tibia length of $833 \pm 38 \mu\text{m}$ ($n = 18$), and those collected in March had a mean hind tibia length of $772 \pm 58 \mu\text{m}$ ($n = 8$). After month of collection had been included in the generalized linear model, there was no relationship between parasitoid body size and egg load ($P = 0.887$).

Time of year was confounded with host density because, during summer, host density increased until either early January (e.g. 1996–1997; Fig. 1) or April (1999–2000; Fig. 1). However, both terms remained significant ($P < 0.001$) when they were both fitted in the regression. As shown in Fig. 5, egg loads declined from a maximum at the onset of adult parasitoid emergence in mid-November to a minimum at the end of the period in which adult parasitoids occurred. This was described by the negative exponential curve, $p = e^{4.37 - 0.0081t}$, where p = parasitoid egg load, and t = time elapsed between 1 November and the sampling date in days (Fig. 5). At $t = 15$ (mid-November), females contained 70 eggs, and at $t = 134$ (mid-March), they contained 27 eggs.

After accounting for variation due to host density and/ or time of year, there was no significant egg load variation between years or between parasitoid generations.

Estimates of slopes for linearly varying parasitoid oviposition rates

Densities of unparasitized hosts exhibited two characteristic patterns of change when female parasitoids were present in the field. Both were consistent with previous observations (Goldson *et al.*, 1998a) and are described below.

The first occurred between mid-December and mid-January, when unparasitized hosts erupted from negligible to very high densities (Fig. 2). The slopes of the mid-December to mid-January increases in unparasitized host densities were 0.16 in 1996–1997, 0.07 in 1997–1998, 0.07 in 1998–1999, and 0.02 in 1999–2000. Thus, we modelled two oviposition rates that increased linearly from zero, with slopes of 0.001 and 0.3, to the maximum of 2 eggs per hour. It was also notable that female parasitoids began emerging 16–33 days before host densities reached their annual minima in mid-December (Fig. 2), and these females could not have reproduced until after host densities began to increase because the few senescing overwintered hosts available before mid-December would not have lived long enough to support immature parasitoid development. Therefore, we also explored how a modest delay of 100 hours between parasitoid emergence and the start of oviposition influenced investments in reproduction.

The second characteristic pattern of change occurred from mid-January to mid-May, when unparasitized host densities declined from their January peaks, though only to moderate levels, which then tended to stabilize and persist during winter (Fig. 2). The slopes of the mid-January to mid-May declines in unparasitized hosts, disregarding 1997–1998 when few parasitoids were captured, were -0.06 in 1996–1997, -0.02 in 1998–1999, and -0.002 in 1999–2000 (Fig. 2). Thus, we modelled two oviposition rates that declined

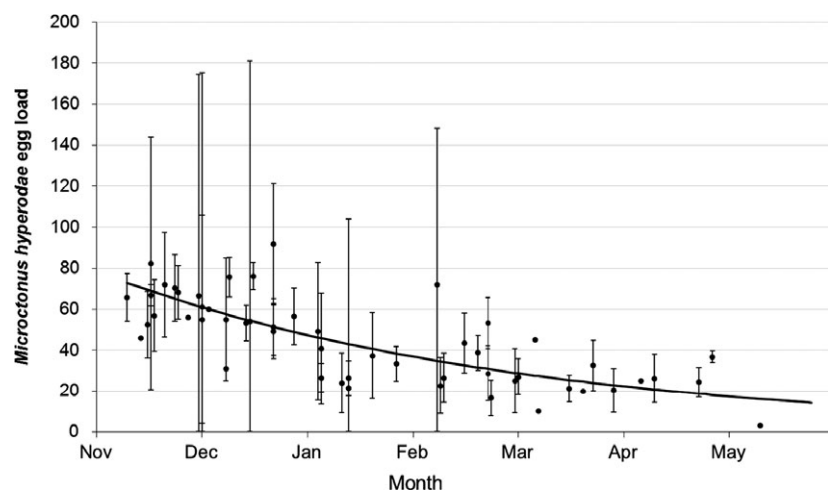


Fig. 5 Regression of *Microctonus hyperodae* egg load with date from 1 November to 30 May during 1996–2000. Points show mean egg load per sample with 95% CI.

linearly from a maximum of 2 eggs per hour, with slopes of -0.001 and -0.1 , to a minimum of 0.05 eggs per hour.

Modelling results

We recovered two general results consistent with previous studies (Ellers *et al.*, 2001; Rosenheim, 2011). The first was that parasitoid investment in eggs and the proportion of females that became egg limited both increased with egg cost (Fig. 6). The second was that investment in eggs increased with oviposition rate (Fig. 6A cf. 6B) as did the proportion of females that became egg limited (Fig. 6C cf. 6D). At our highest linearly increasing oviposition rate, which had a slope of $+0.3$, we obtained results for optimal investment in

reproduction (Fig. 6A) and proportion of females that are egg limited (Fig. 6C) that were essentially identical to the results obtained by Rosenheim (2011) using a constant oviposition rate of 1 egg per hour.

We also obtained several new results: the first two reflect the intuitively straightforward expectation that females experiencing delays to oviposition will experience stronger selection pressure for longer lifespans. The less straightforward aspect of these results is how temporal stochasticity influenced evolutionarily optimal investments in eggs.

The first new result was that when oviposition rate increased only slowly (slope = $+0.001$), investment in eggs peaked at an intermediate level of temporal stochasticity (Fig. 6B), as did the proportion of females that became egg limited (Fig. 6D). Short-lived

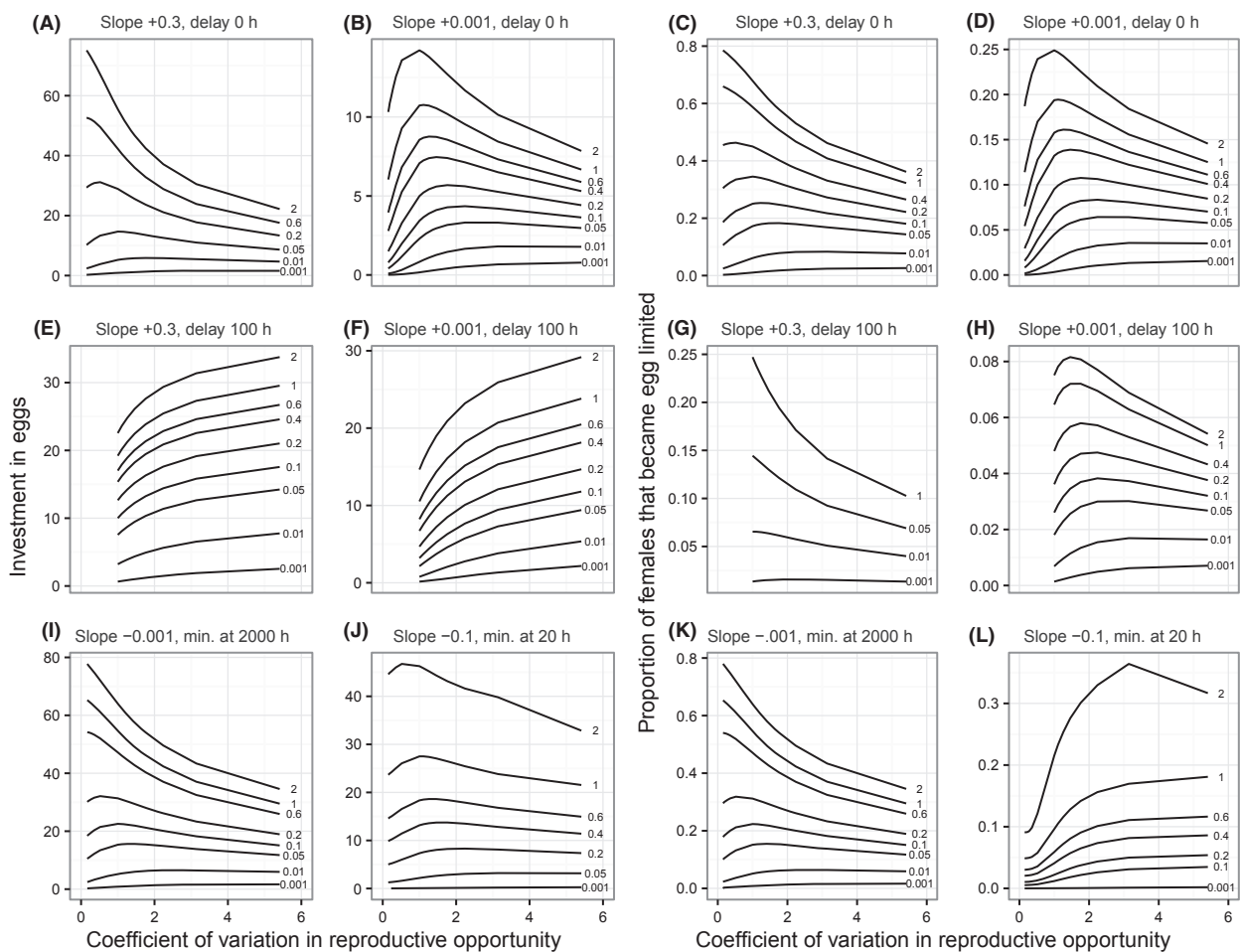


Fig. 6 Results from model of Rosenheim (2011) modified to simulate linearly increasing and decreasing oviposition rates. Six left-most graphs show relationship between optimal resource allocation to eggs and coefficient of variation for temporal stochasticity. Six right-most graphs show relationship between proportion of females that became egg limited and coefficient of variation for temporal stochasticity. Within each graph, lines show responses at different egg costs. Graphs A–D have increasing linear oviposition rates with zero delay between emergence and oviposition; graphs E–H have increasing linear oviposition rates with delays between emergence and oviposition; graphs I–L have decreasing linear oviposition rates. Note that the y-axis scales vary between graphs.

parasitoids had a low probability of encountering hosts when stochasticity was minimal, so invested in lifespan. The probability of encountering hosts first increased with stochasticity, allowing greater investment in eggs, then declined again as short lifespans became penalized by high stochasticity. Previous research has recorded only a negative relationship between temporal stochasticity and investment in eggs (Rosenheim, 2011).

The second new result was that the positive response of investment in eggs to temporal stochasticity was intensified by delays between emergence and the start of oviposition (Fig. 6E,F). When temporal stochasticity was minimal, no females survived the delay to oviposit and optimal egg investments were undefined (Fig. 6E, F). Once temporal stochasticity was sufficient for females to encounter hosts, investment in eggs increased with increasing stochasticity, though at a declining rate (Fig. 6E,F). Investment in eggs showed a stronger positive response to stochasticity when oviposition rates increased slowly rather than quickly (Fig. 6F cf. 6E).

The less straightforward aspect of the new results reflects the observation that females experiencing rapidly declining oviposition rates will have restricted capacity to optimize fitness (Fig. 6I–L). This is because the marginal fitness gains obtainable from trading off investments in eggs and lifespan are strongly limited by the forthcoming low constant oviposition rate. When oviposition rate declined very slowly, investment in eggs (Fig. 6I) and the proportion of females that became egg limited (Fig. 6K) responded to increasing stochasticity similarly to when oviposition rate either increased quickly (Fig. 6A,C) or was constant (Rosenheim, 2011; approximated by Figs 6A and 5C). However, when oviposition rate declined quickly, investment in eggs responded weakly to temporal stochasticity only at the highest egg cost (Fig. 6J) and, unlike any other scenario, the proportion of females that became egg limited tended to increase with temporal stochasticity (Fig. 6L).

Discussion

Our field results showed that egg loads of an insect parasitoid were negatively correlated with host population density, thus contributing to scarce empirical support (Phillips *et al.*, 1998; Segoli & Rosenheim, 2013; Dieckhoff *et al.*, 2014) for theoretical expectations that egg limitation risks should increase with host encounter rate (Rosenheim, 1996; Mangel & Heimpel, 1998; Sevenster *et al.*, 1998; Ellers *et al.*, 2000; Gandon *et al.*, 2009). Our model results revealed that host population dynamics can interact with temporal stochasticity to influence evolution of parasitoid egg load in previously unrecognized ways. In particular, resource allocations to eggs may increase with temporal stochasticity whenever parasitoids either experience delays between

emergence and oviposition, or experience low host availability that increases only slowly. These responses to temporal stochasticity would act in concert with spatial stochasticity, which also favours resource allocations to eggs over lifespan (Godfray, 1994; Ellers *et al.*, 2000; Rosenheim, 2011), and contribute to the generally low rates of egg limitation observed in empirical studies (Heimpel & Rosenheim, 1998). Together, our field and model results showed that host population dynamics, and their interactions with temporal stochasticity, impose conflicting selection pressures on females and their offspring within a single season.

Some parasitoid species that experience seasonally varying selection pressures have evolved seasonally varying reproductive strategies (Godfray & Shaw, 1987; Sequeira & MacKauer, 1993; Ellers *et al.*, 2001), but no such adaptations have been recognized in *M. hyperodae*. Indeed, results from the current and previous studies suggest *M. hyperodae* females allocate similar resources to eggs irrespective of the time of year they emerge. The first evidence for this comes from comprehensive laboratory studies of *M. hyperodae* pre-oviposition egg load, which detected no seasonal variation (Phillips & Baird, 2001; Urrutia *et al.*, 2007). Moreover, although laboratory studies found a weak relationship between egg load and female size (Phillips & Baird, 2001), and our field measurements indicated that female parasitoid size declined slightly between spring and autumn, we found no relationship between body size and egg load in the field data. This was unsurprising due both to the greater variation inherent in field studies compared to laboratory studies and to the minor effect on egg load that the observed small size difference would have. For example, based on the relationship between egg load and female size measured in laboratory-reared *M. hyperodae* (Phillips & Baird, 2001), the difference in mean pre-oviposition egg load between the larger females present in spring and the smaller females present in autumn would only be about four eggs. Also, previous laboratory studies (Phillips & Baird, 2001; Urrutia *et al.*, 2007; C.B. Phillips unpublished data) indicate that *M. hyperodae* pre-oviposition egg load responds positively, though weakly, to the temperature at which its immature stages develop. Females sampled during mid-summer–autumn will have developed at higher mean temperatures than those sampled during spring–early summer, thus acting to compensate for any reduction in egg load due to smaller body size. Finally, after accounting for variation due to host density and/or time of year, our analysis found no significant egg load variation between spring–early summer and mid-summer–autumn. Indeed, females with the highest egg loads in our field study had probably laid few or no eggs, and the highest egg loads recorded during mid-summer–autumn were similar to those recorded in spring–early summer (Fig. 4). Thus, we conclude that *M. hyperodae* females allocate similar resources to eggs irrespective of the time of year they emerge.

This conclusion is conservative for our study because the most plausible alternative is that mid-summer–autumn parasitoids (which experience abundant hosts) should emerge with more eggs than spring–early summer parasitoids (which experience few hosts). Nevertheless, we observed that mid-summer–autumn parasitoids have lower post-emergence egg loads. Thus, if allocations to eggs were assumed to be greater during mid-summer–autumn, then our empirical evidence that mid-summer–autumn parasitoids experience higher oviposition rates would be even stronger. Our conclusion of similar allocations to eggs across seasons is important to the following considerations of responses by *M. hyperodae* to seasonally varying selection pressures.

In spring, *M. hyperodae* females begin emerging well before their hosts. Consequently, they coincide with very low host densities, experience low oviposition rates and are at high risk of time limitation. Such asynchrony between parasitoids and their hosts appears common (e.g. Griffiths, 1969; Weseloh, 1976; Cameron & Walker, 2002; van Nouhuys & Lei, 2004; Evans *et al.*, 2013). Selection favouring females with long lifespans must be stringent in this situation, so why do *M. hyperodae* females that emerge in spring apparently allocate as many resources to eggs as their summer offspring do, thus possessing many more eggs than they can usually lay (e.g. Fig. 4)? First, as shown by our modelling, temporal stochasticity in reproductive opportunity will favour investment in eggs, as will spatial stochasticity (Godfray, 1994; Eilers *et al.*, 2000; Rosenheim, 2011). Second, some parasitoid adaptations for extending lifespan such as feeding on floral nectar will incur minimal costs for egg production and lifetime fecundity if, due to early parasitoid emergence and an absence of hosts, time spent foraging reduces neither the rate of oviposition nor survival (e.g. through increased predation risk). Indeed, *M. hyperodae* possesses this adaptation, but is usually unable to capitalize on it due to the frequent absence of suitable nectar sources from New Zealand pastures (Vattala, 2005; C.B. Phillips, unpublished data). This was clearly shown by replicated controlled field experiments that provided *M. hyperodae* females with floral nectar (flowering buckwheat) within otherwise typical New Zealand pasture (Vattala, 2005). With access to nectar, early emerging *M. hyperodae* doubled their reproduction (measured as the proportion of hosts parasitized), which confirmed that early emerging *M. hyperodae* are mostly time limited (Vattala, 2005). Thus, evolution of foraging by *M. hyperodae* probably mitigated some of the cost of early emergence and, in tandem with spatial and temporal stochasticity in reproductive opportunity, reduced selection for greater resource allocations to lifespan at the expense of eggs. Possible benefits of early emergence in *M. hyperodae* are discussed later.

Females present in summer coincided with much higher host densities and were at greater risk of egg

limitation. This was consistent with the previously described field experiment (Vattala, 2005), which recorded no increase in *M. hyperodae* reproduction when females were provided access to nectar during summer. Under such conditions, selection favouring investment in eggs over lifespan would be reinforced by spatial stochasticity in reproductive opportunity (Rosenheim, 2011), but moderated by temporal stochasticity.

Females present after mid-February coincided with declining host densities. The model results showed that when these declines are abrupt, the marginal gains in fitness obtainable by trading off investments in eggs and lifespan are restricted by the ensuing low constant oviposition rate; long-lived females lay scarcely more eggs than short-lived females, thus responses to temporal stochasticity are weak.

As described above, previous studies combined with our field observations and model results provide rationales for the apparent absence of a seasonally varying reproductive strategy in *M. hyperodae*, despite the existence of seasonally varying selection pressures. (Another plausible rationale is that the *M. hyperodae*'s responses to these pressures are constrained; Hoffmann, 2014.) Nevertheless, the early emergence of *M. hyperodae* females in spring, up to 33 days before hosts become available in early summer, appears maladaptive at first glance. Could it have benefits? It is possible that spring-emerging *M. hyperodae* females gain fitness by trading their early season fecundity for the late season survival of their offspring. Each season, *M. hyperodae* experiences strong developmental time constraints because it can survive the next winter only as an egg or larva (Fig. 1; Barlow *et al.*, 1994; Goldson *et al.*, 1998b). Thus, parasitoid larvae that emerge from their hosts in autumn are at risk of being killed by cold weather before they can reach the adult stage and find new hosts in which to oviposit offspring that will survive the winter. By emerging in spring, females risk dying before their hosts emerge and appear irrevocably destined to achieve only low fecundity (Fig. 4). However, their late summer offspring may gain fitness because host availability and parasitoid fecundity are high, and the risk of mortality due to cold weather is reduced. In some seasons, the offspring of first-emerging parasitoids might even achieve an extra generation during summer and autumn. Fitness advantages for spring-emerging females would be greater in seasons when lethally cold conditions arrive relatively early in autumn, whereas later emerging females would benefit from prolonged warm autumns (provided the warm conditions ended before descendants of spring-emerging parasitoids could complete an additional generation). Thus, 'adaptive asynchrony' (Singer & Parmesan, 2010) is a possibility worthy of further investigation in *M. hyperodae*. Under this hypothesis, *M. hyperodae* females emerging in spring, which are at risk of time

limitation (Fig. 4), would make a larger contribution to total population reproduction by the end of autumn than females emerging during summer, which are at greater risk of egg limitation (Fig. 4). This population dynamics perspective differs slightly from Rosenheim (2011) which, from the viewpoint of purely stochastic variation in reproductive success, emphasized how it was egg limited parasitoids that made the major contribution to total reproduction.

Monitoring of host density through time demonstrated the existence of considerable temporal variability in host abundance, thus illustrating the scenario modelled by Rosenheim (2011) where trade-offs favouring parasitoid reproduction over survival during periods of high host abundance can be strongly penalized during periods of low host abundance when traits such as longer lifespan or larger egg size would be more successful. However, host seasonality is partly predictable and must be a critical evolutionary driver for many parasitoid species (Forrest & Miller-Rushing, 2010), particularly specialists that depend on one or a few host species to reproduce. Our study indicates that understanding the evolution of parasitoid egg load would benefit from a shift of research emphasis from purely stochastic variation in parasitoid reproductive opportunities to greater consideration of host dynamics.

Acknowledgments

We thank Jay Rosenheim (University of California, Davis) and two anonymous reviewers for helpful comments on an earlier version of this manuscript, David Baird (VSN New Zealand Ltd) for assistance with statistical analyses, and John Proffitt, Rachel Cane and Katrin Schöps (AgResearch, Lincoln) for help with field sampling and parasitoid dissections. The research was funded through the MBIE contract LINX0804, Ecosystem Bioprotection. The authors declare no conflict of interests.

References

- Anonymous. 2010. *Environmental Snapshot: Land Use*. New Zealand Ministry for the Environment, Wellington. 6 pp.
- Armstrong, S.M., Barratt, B.I.P. & Evans, A.A. 1996. Circadian pattern of oviposition in the two parasitoids *Microctonus aethiopoidea* Loan and *M. hyperodae* Loan (Hymenoptera: Braconidae), in relation to host activity. *Proceedings of the 49th New Zealand Plant Protection Conference* 49, pp. 280–284.
- Barlow, N.D., Goldson, S.L. & McNeill, M.R. 1994. A prospective model for the phenology of *Microctonus hyperodae*, a potential biological control agent of Argentine stem weevil in New Zealand. *Biocontrol Sci. Tech.* **4**: 375–386.
- Barratt, B.I.P., Evans, A.A., Ferguson, C.M., Barker, G., McNeill, M.R. & Phillips, C.B. 1997. Laboratory nontarget host range of the introduced parasitoids *Microctonus aethiopoidea* and *M. hyperodae* (Hymenoptera: Braconidae) compared with field parasitism in New Zealand. *Environ. Entomol.* **26**: 694–702.
- Bernstein, C. 2000. Host-parasitoid models: the story of a successful failure. In: *Parasitoid Population Biology* (M.E. Hochberg & A.R. Ives, eds), pp. 41–57. Princeton University Press, Princeton, NJ.
- Cameron, P.J. & Walker, G.P. 2002. Field evaluation of *Cotesia rubecula* (Hymenoptera: Braconidae), an introduced parasitoid of *Pieris rapae* (Lepidoptera: Pieridae) in New Zealand. *Environ. Entomol.* **31**: 367–374.
- Casas, J., Nisbet, R.M., Swarbrick, S. & Murdoch, W.W. 2000. Eggload dynamics and oviposition rate in a wild population of a parasitic wasp. *J. Anim. Ecol.* **69**: 185–193.
- Casas, J., Vannier, F., Mandon, N., Delbecq, J.P., Giron, D. & Monge, J.P. 2009. Mitigation of egg limitation in parasitoids: immediate hormonal response and enhanced oogenesis after host use. *Ecology* **90**: 537–545.
- Dieckhoff, C., Theobald, J.C., Wäckers, F.L. & Heimpel, G.E. 2014. Egg load dynamics and the risk of egg and time limitation experienced by an aphid parasitoid in the field. *Ecol. Evol.* **4**: 1739–1750.
- Ellers, J., Sevenster, J.G. & Driessen, G. 2000. Egg load evolution in parasitoids. *Am. Nat.* **156**: 650–665.
- Ellers, J., Bax, M. & van Alphen, J.J.M. 2001. Seasonal changes in female size and its relation to reproduction in the parasitoid *Asobara tabida*. *Oikos* **92**: 309–314.
- Evans, E.W., Carlile, N.R., Innes, M.B. & Pitigala, N. 2013. Warm springs reduce parasitism of the cereal leaf beetle through phenological mismatch. *J. Appl. Entomol.* **137**: 383–391.
- Fernández-Arhex, V. & Corley, J.C. 2003. The functional response of parasitoids and its implications for biological control. *Biocontrol Sci. Tech.* **13**: 403–413.
- Forkner, R.E., Marquis, R.J., Lill, J.T. & Corff, J.L. 2008. Timing is everything? Phenological synchrony and population variability in leaf-chewing herbivores of *Quercus*. *Ecol. Entomol.* **33**: 276–285.
- Forrest, J. & Miller-Rushing, A.J. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Phil. Trans. R. Soc. B Biol. Sci.* **365**: 3101–3112.
- Gandon, S., Varaldi, J., Fleury, F. & Rivero, A. 2009. Evolution and manipulation of parasitoid egg load. *Evolution* **63**: 2974–2984.
- Genstat Committee. 2002. *The Guide to Genstat Part 2: Statistics*. VSN International, Oxford.
- Godfray, H.C.J. 1994. *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton University Press, Princeton, NJ.
- Godfray, H.C.J. & Shaw, M.R. 1987. Seasonal variation in the reproductive strategy of the parasitic wasp *Eulophus larvarum* (Hymenoptera: Chalcidoidea: Eulophidae). *Ecol. Entomol.* **12**: 251–256.
- Godfray, H.C.J., Hassell, M.P. & Holt, R.D. 1994. The population dynamic consequences of phenological asynchrony between parasitoids and their hosts. *J. Anim. Ecol.* **63**: 1–10.
- Goldson, S.L., McNeill, M.R., Proffitt, J.R. & Hower, A.A. 1995. An investigation into the reproductive characteristics of *Microctonus hyperodae* (Hymenoptera: Braconidae), a parasitoid of *Listronotus bonariensis* (Kuschel) (Col.: Curculionidae). *Entomophaga* **40**: 413–426.
- Goldson, S.L., Proffitt, J.R. & Baird, D.B. 1998a. The bionomics of *Listronotus bonariensis* (Coleoptera: Curculionidae) in Canterbury, New Zealand. *Bull. Entomol. Res.* **88**: 415–423.
- Goldson, S.L., Proffitt, J.R. & Baird, D.B. 1998b. Establishment and phenology of the parasitoid *Microctonus hyperodae* (Hymenoptera: Braconidae) in New Zealand. *Environ. Entomol.* **27**: 1386–1392.

- Griffiths, K.J. 1969. The importance of coincidence in the functional and numerical responses of two parasites of the European pine sawfly, *Neodiprion sertifer*. *Can. Entomol.* **101**: 673–713.
- Heimpel, G.E. & Rosenheim, J.A. 1998. Egg limitation in parasitoids: a review of the evidence and a case study. *Biol. Control* **11**: 160–168.
- Hoffmann, A. 2014. *Evolutionary Limits and Constraints. The Princeton Guide to Evolution*. Princeton University Press, Princeton, NJ, pp. 247–252.
- Iline, I.I. & Phillips, C.B. 2004. Allozyme markers to help define the South American origins of *Microctonus hyperodae* (Hymenoptera: Braconidae) established in New Zealand for biological control of Argentine stem weevil. *Bull. Entomol. Res.* **94**: 229–234.
- Jervis, M.A., Kidd, N.A.C. & Heimpel, G.E. 1996. Parasitoid adult feeding behaviour and biocontrol - a review. *Biocontrol News Inf.* **17**: 11–25.
- Jervis, M.A., Heimpel, G.E., Ferns, P.N., Harvey, J.A. & Kidd, N.A.C. 2001. Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. *J. Anim. Ecol.* **70**: 442–458.
- Loan, C.C. & Lloyd, D.C. 1974. Description and field biology of *Microctonus hyperodae* Loan n. sp. (Hymenoptera: Braconidae, Euphorinae) a parasite of *Hyperodes bonariensis* in South America (Coleoptera: Curculionidae). *Entomophaga* **19**: 7–12.
- Mangel, M. & Heimpel, G.E. 1998. Reproductive senescence and dynamic oviposition behaviour in insects. *Evol. Ecol.* **12**: 871–879.
- McCullagh, P. & Nelder, J.A. 1983. *Generalised Linear Models*. Chapman and Hall, London.
- McNeill, M.R., Goldson, S.L. & Baird, D.B. 1996. Evidence of host discrimination by *Microctonus hyperodae* Loan (Hym.: Braconidae, Euphorinae), a parasitoid of the Argentine stem weevil *Listronotus bonariensis* (Kuschel) (Col.: Curculionidae). *Biocontrol Sci. Technol.* **6**: 77–89.
- van Nouhuys, S. & Lei, G. 2004. Parasitoid–host metapopulation dynamics: the causes and consequences of phenological asynchrony. *J. Anim. Ecol.* **73**: 526–535.
- Papaj, D.R. 2000. Ovarian dynamics and host use. *Annu. Rev. Entomol.* **45**: 423–448.
- Phillips, C.B. 2002. Observations of oviposition behavior of *Microctonus hyperodae* Loan and *M. aethiopoidea* Loan (Hymenoptera: Braconidae: Euphorinae). *J. Hymenopt. Res.* **11**: 326–337.
- Phillips, C.B. & Baird, D.B. 2001. Geographic variation in egg load of *Microctonus hyperodae* Loan (Hymenoptera: Braconidae) and its implications for biological control success. *Biocontrol Sci. Technol.* **11**: 371–380.
- Phillips, C.B., Proffitt, J.R. & Goldson, S.L. 1998. Potential to enhance the efficacy of *Microctonus hyperodae* Loan. *Proceedings of the New Zealand Plant Protection Conference* 51, pp. 16–22.
- Phillips, C.B., Baird, D.B., Iline, I.I., McNeill, M.R., Proffitt, J.R., Goldson, S.L. *et al.* 2008. East meets West: adaptive evolution of an insect introduced for biological control. *J. Appl. Ecol.* **45**: 948–956.
- Proffitt, J.R., Ferguson, C.M., McNeill, M.R., Goldson, S.L., Macnab, H.R. & Barratt, B.I.P. 1993. A comparison of sampling methods for adult *Listronotus bonariensis* (Kuschel). pp. 67–72. In *Proceedings of the 6th Australasian Grassland Invertebrate Ecology Conference*, AgResearch, Ruakura Agricultural Centre, Hamilton.
- R Core Team. 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/> (Accessed September 2013).
- Richard, R. & Casas, J. 2009. Stochasticity and controllability of nutrient sources in foraging: host-feeding and egg resorption in parasitoids. *Ecol. Monogr.* **79**: 465–483.
- Rosenheim, J.A. 1996. An evolutionary argument for egg limitation. *Evolution* **50**: 2089–2094.
- Rosenheim, J.A. 1999. The relative contributions of time and eggs to the cost of reproduction. *Evolution* **53**: 376–385.
- Rosenheim, J.A. 2000. Egg maturation, egg resorption and the costliness of transient egg limitation in insects. *Proc. R. Soc. Lond. B* **267**: 1565–1673.
- Rosenheim, J.A. 2011. Stochasticity in reproductive opportunity and the evolution of egg limitation in insects. *Evolution* **65**: 2300–2312.
- Rosenheim, J.A., Jepsen, S.J., Matthews, C.E., Smith, D.E. & Rosenheim, M.R. 2008. Time limitation, egg limitation, the cost of oviposition, and lifetime reproduction by an insect in nature. *Am. Nat.* **172**: 486–496.
- Segoli, M. & Rosenheim, J.A. 2013. Limits to the reproductive success of two insect parasitoid species in the field. *Ecology* **94**: 2498–2504.
- Sequeira, R. & MacKauer, M. 1993. Seasonal variation in body size and offspring sex ratio in field populations of the parasitoid wasp, *Aphidius ervi* (Hymenoptera: Aphidiidae). *Oikos* **68**: 340–346.
- Sevenster, J., Ellers, J. & Driessen, G. 1998. An evolutionary argument for time limitation. *Evolution* **52**: 1241–1244.
- Shaw, M.R. & Huddleston, T. 1991. *Classification and Biology of Braconid Wasps (Hymenoptera: Braconidae)*. Royal Entomological Society of London, London.
- Singer, M.C. & Parmesan, C. 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Phil. Trans. R. Soc. B Biol. Sci.* **365**: 3161–3176.
- Stireman, J.O., Dyer, L.A., Janzen, D.H., Singer, M.S., Lill, J.T., Marquis, R.J. *et al.* 2005. Climatic unpredictability and parasitism of caterpillars: implications of global warming. *Proc. Natl. Acad. Sci. USA* **102**: 17384–17387.
- Urrutia, C.M.A., Wade, M.R., Phillips, C.B. & Wratten, S.D. 2007. Influence of host diet on parasitoid fitness: unravelling the complexity of a temperate pastoral agroecosystem. *Entomol. Exp. Appl.* **123**: 63–71.
- Van Baalen, M. 2000. The evolution of parasitoid egg load. In: *Parasitoid Population Dynamics* (M. Hochberg & A. R. Ives, eds), pp. 103–120. Princeton University Press, Princeton.
- Vattala, H.D. 2005. Enhancement of the efficacy of the parasitoid, *Microctonus hyperodae* Loan (Hymenoptera: Braconidae) by provision of floral resources to improve biological control of its host, the Argentine stem weevil (*Listronotus bonariensis*) (Kuschel) (Coleoptera: Curculionidae). Unpublished Ph.D. thesis, Lincoln University, Lincoln.
- Vattala, H.D., Wratten, S.D., Phillips, C.B. & Wäckers, F.L. 2006. The influence of flower morphology and nectar quality on the longevity of a parasitoid biological control agent. *Biol. Control* **39**: 179–185.
- Weseloh, R.M. 1976. Reduced effectiveness of the gypsy moth parasite, *Apanteles melanoscelus*, in Connecticut due to poor seasonal synchronization with its host. *Environ. Entomol.* **5**: 743–746.

Received 14 October 2016; accepted 12 April 2017