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Contrasting host: parasitoid synchrony drives differing levels of biocontrol by two introduced *Microctonus* spp. in northern New Zealand pastures

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Abstract Two species from the genus *Microctonus* Wesmael (Hymenoptera: Braconidae) have been introduced into New Zealand as biocontrol agents of pest weevils in pasture. Both parasitoids have similar life cycles and co-exist in pasture along with their respective weevil hosts. However, winter parasitism rates by *M. hyperodae* Loan are low in comparison to the Irish biotype of M. aethiopoides' Loan. Population studies at two Waikato sites over three consecutive seasons of parasitoid activity showed that *M. aethiopoides* recovered from near extinction each spring and built up to effective levels by winter because hosts were available continuously throughout summer and autumn. In contrast, *M. hyperodae* began each season at higher larval populations and parasitism levels than *M. aethiopoides*, but populations and parasitism levels declined during late summer and early autumn due to low host availability. The contrast between species is consistent with the high levels of endophyte-conferred pest-resistant grass in the pastures, which impacts strongly on *M. hyperodae*'s host weevil abundance during summer but has no effect on *M. aethiopoides*' host weevils which feed only on clovers. It was accentuated by a warming climate with the now regular occurrence of a third host generation after most *M. hyperodae* adult activity had ceased.

Keywords Asynchrony · Climate · *Sitona obsoletus* · *Microctonus hyperodae* · Endophyte · *Microctonus aethiopoides* · *Listronotus bonariensis*

Introduction

A key criterion to the success of classical biocontrol is how well the introduced natural enemies synchronise with the susceptible host stages in the novel environment (Mills 2018). However, synchrony can be disrupted by environmental changes. Such perturbations occur naturally through annual variations in temperature (van Nouhuys and Lei 2004), and weather events such as flood and droughts, but are inherent in agricultural landscapes, where host-parasitoid relationships may be disrupted by agricultural practices (Tooker et al. 2020). The relative simplicity of the New Zealand pasture ecosystem and introduced biocontrol agent food webs therein (Goldson et al. 2020) provide an opportunity to observe how an agricultural practice may disrupt host-parasitoid synchrony. The pastures consist almost entirely of

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introduced *Lolium* L. and *Trifolium* L. species. Two very similar parthenogenetic species from the genus *Microctonus* Wesmael (Hymenoptera: Braconidae) have been introduced into New Zealand as biocontrol agents for exotic pasture weevil (Coleoptera: Curculionidae) pests. They have almost identical life cycles. The endoparasitoids attack the adult weevils and their hosts have two to three generations per year. Both parasitoids diapause as first instar larvae within their overwintering adult hosts and have several generations during the warmer months. They coexist in pastures, along with their respective target hosts.

An Irish biotype of *M. aethiopoides* Loan was released in 2006 for the control of the clover root weevil *Sitona obsoletus* (Gmelin), a pest that attacks only *Trifolium* spp., particularly white clover *T. repens* L. (Gerard et al. 2007). Establishment was rapid with overwintering parasitism in weevil adults at or exceeding 70% the year following release (Gerard et al. 2011). The parasitoid proved to be facultative gregarious in the field with often two or three larvae per host when parasitism levels were high (Gerard et al. 2007). High overwintering parasitism levels are essential to control this fecund pest as it is the weevil larvae originating from this generation of adults that have the severest impact on clover performance and subsequent animal production (Gerard et al. 2010).

Microctonus hyperodae Loan was introduced from South America and released at various sites in the early 1990s (Goldson et al. 1990; McNeill et al. 2002). The target is the Argentine stem weevil *Listronotus bonariensis* (Kuschel), a pest that attacks a wide range of cereals and grasses, including weed species. Initial establishment at release sites was excellent with overwintering parasitism rates exceeding 75% within three years of release (Barker and Addison 2006; Goldson et al. 1998). However, overwintering parasitism rates have tracked downwards since then (Goldson and Tomasetto 2016; Goldson et al. 2014b; Tomasetto et al. 2018a) and notable weevil damage has been evident in susceptible pastures (Popay et al. 2011). This decline in parasitism rates of a classical biocontrol agent is highly unusual (Goldson et al. 2014a) and there is concern that, because of the multiple similarities in seasonality, biology and ecology, the Irish *M. aethiopoides* biotype may be vulnerable also. While most sown perennial, annual and hybrid ryegrasses have protection against Argentine stem weevil through the alkaloids produced by different strains of the endophyte *Epichloë festucae* var. *lolii* (Thom et al., 2014), there is no other economic or environmentally acceptable means of protecting white clover in New Zealand pastures than through parasitism of the host by *M. aethiopoides*. To date, no clear cause for the decline in *M. hyperodae* parasitism rates has been identified although evolved resistance by the weevil has been hypothesised due to the high levels of heterozygosity in Argentine stem weevil populations (Harrop et al. 2020). Using a set of time series analyses and historic overwintering parasitism data from three distinct regions, Tomasetto et al. (2018b) showed elapsed time since release was the most prevalent influence, which aligns with the resistance hypothesis (Casanovas et al. 2018; Tomasetto et al. 2017). However, it is also known that multitrophic interactions with pasture grasses exist, with *M. hyperodae* parasitism rate inversely related to ppm of peramine in pasture, an alkaloid produced by the ryegrass endophyte (Goldson et al. 2000), and higher parasitism in tetraploid compared to diploid ryegrass swards (Goldson et al. 2015). Furthermore, both *M. hyperodae* and *M. aethiopoides* are disrupted by summer drought (Gerard et al. 2012) and warmer temperatures have been shown to increase alkaloid production in endophyte-infected ryegrass (Hennessy et al. 2016). We hypothesised that multitrophic interactions associated with endophytic ryegrass disrupts host availability during summer, and the resultant asynchrony contributes to the decline in *M. hyperodae* parasitism rates.

This article reports on population studies on *M. hyperodae* and Irish *M. aethiopoides*, and their respective hosts that were carried out in the Waikato region from 2011 to 2015. This region, New Zealand has warm humid summers and mild winters. We compare this new *M. hyperodae* data with Argentine stem weevil and *M. hyperodae* data collected 1991–1996 in Waikato (Barker 2013; Barker and Addison 2006) soon after the parasitoid's release.

Materials and methods

Insect sampling

Monthly sampling of weevil adult populations was carried out at a site at Springdale, Morrinsville, New Zealand (37°31′56″ S, 175°33′6″ E) where Irish *M.*

aethiopoides had been released in January 2006 (Gerard et al. 2011), and at the Ruakura Research Centre farm, Hamilton, New Zealand (37°46′01.5″ S 175°19′09.5″ E) where it was released in January 2007. Both pastures were predominantly ryegrass/white clover and over ten years old. However, the former was high fertility dairy pasture and the latter lower quality pasture mainly grazed by sheep. Ryegrass endophyte infection levels were high at both sites (98% at Morrinsville and 94% at Ruakura in October 2013). The endophyte type was unknown. Monthly pasture composition data were collected but results are not presented.

Insect sampling commenced in September 2011 (early spring) and finished in June 2014 (early winter), thus encompassing three cycles of parasitoid activity and diapause. Weevil population density sampling consisted of four 30 × 0.1 m suction samples using a modified Dolmar PB250 blower vac taken at random transects across each site. To increase the likelihood that at least 20 weevils of each species were collected, and therefore the accuracy of parasitism assessments, an additional bulk sample was collected by 5 min suction over patches of favoured vegetation likely to be weevil "hotspots" in the pasture. Weevils were hand-sorted from the suction samples in the laboratory, sealed in small zip locked plastic bags with a sample label, then stored in a freezer at − 20 °C. The weevils were dissected under a binocular microscope and the number and life stages of any parasitoids present were recorded. Weevil population densities were calculated from the suction samples, and parasitoid larval densities from the weevil density, percent parasitism and parasitoid larvae/weevil data.

Comparison with historic data

To compare the seasonal patterns of current and 1990s Argentine stem weevil populations and parasitism levels, data was utilised from the Ruakura 1991 *M. hyperodae* release site (Barker 2013) for the period May 1993–May 1996, at which time the parasitoid was well established and parasitism rates during winter had reached seasonal maxima of 75–90%. Climate data was obtained from the National Climate Database (CliFlo 2020).

Data analysis

The weevil and parasitoid densities (Supplementary figures S1 and S2) were analysed using Bayesian smoothing techniques in Flexi (Upsdell 1994) with a log link function. Bayesian statistics were used as the investigation was into a predator-prey relationship and the associated time lag. The added advantage is that the results of the analyses are presented as figures with 5% least significance interval bands which are more easily assimilated than extensive tables as they allow the reader to easily see where two curves are significantly different by noting where the bands do not overlap. Note, the term 'band' is used in conjunction with 'interval' as the analyses explicitly modelled the correlation induced by measuring the same paddocks repeatedly over time, rather than undertaking separate analyses at each time point. The time data was modelled as a seasonal component plus a long-term component. The seasonal component had a cyclic covariance function, and the long-term component had a twice integrated Gaussian covariance function. The date for the parasitoid had a lag subtracted from it. The size of the lag was estimated by maximum likelihood when computing the parameters of the mixed model smoother. The model fitted was: Density = (Long-term + Season) × Site × Insect + Sample. Site denotes either Morrinsville or Ruakura; Insect denotes either parasitoid or host Sample is a factor with a separate level for each record. The date variable was divided into a seasonal effect which repeated exactly every year, and a long-term effect which did not. All model terms have a random component. The categorical variables in this study have only two levels so whether they are fixed or random makes no difference. The auto-correlations commonly found when repeatedly measuring the same site have been removed by explicitly modelling the separate site curves. The residual error is composed of two terms. There is the error term Sample which accounts for day-to-day differences in the true counts. In addition, there is the measurement error due to suctioning only a limited area. This measurement error was modelled as a Poisson error of counts per area sampled. Sampling a larger area of the paddock would reduce the size of the Poisson error but the size of the Sample error would remain the same.

The species differences in parasitism were analysed using the same Bayesian smoothing technique

(Upsdell 1994). The model fitted was: % Parasitised = (Long-term + Season) × (Species + Site) + Sample. Species denotes either the clover root weevil, *M. aethiopoides* or the Argentine stem weevil, *M. hyperodae* combinations; Site denotes either Morrinsville or Ruakura; and Sample is a factor with a separate level for each record. The measurement error was modelled as a Binomial error.

Results

Seasonal patterns of abundance

At both the Morrinsville and Ruakura sites (Fig. 1), a minor outbreak of clover root weevil over the first summer and autumn was followed by large peak in *M. aethiopoides* larval populations in late autumn (May 2012). This led to low recruitment for the following summer weevil generation (December 2013). Both host adult and parasitoid larval populations were low in winter 2013 and remained low until the end of the study in June 2014. Both sites had similar clover root weevil and *M. aethiopoides* larval populations initially, but Morrinsville had significantly higher numbers of both species in early 2013 and 2014 (Fig. 1). *M. aethiopoides* larval populations usually exceeded host populations over winter when parasitism levels were high and multiple larvae per host were the norm. The analysis indicated a delayed density dependent interaction between host and parasitoid with the parasitoid peaking 34 ± 20 days after the host.

The seasonal pattern of clover root weevil adult abundance was identical to that described at these sites from 1996 to 2005 prior to parasitoid release, albeit lower than the 100 m^{-2} plus population densities found using the same sampling methods during that time (Gerard et al. 2010). Generation 1 weevil adults that arose from eggs laid in late autumn and winter peaked in mid-summer (late December/early January) and the overwintering generation 2 adults peaked in autumn (late March–early April). While clover root weevil adults in generations 1 and 2 overlapped during summer, there was a two-month period of adult scarcity (September–October) between overwintering adults and those emerging in late spring.

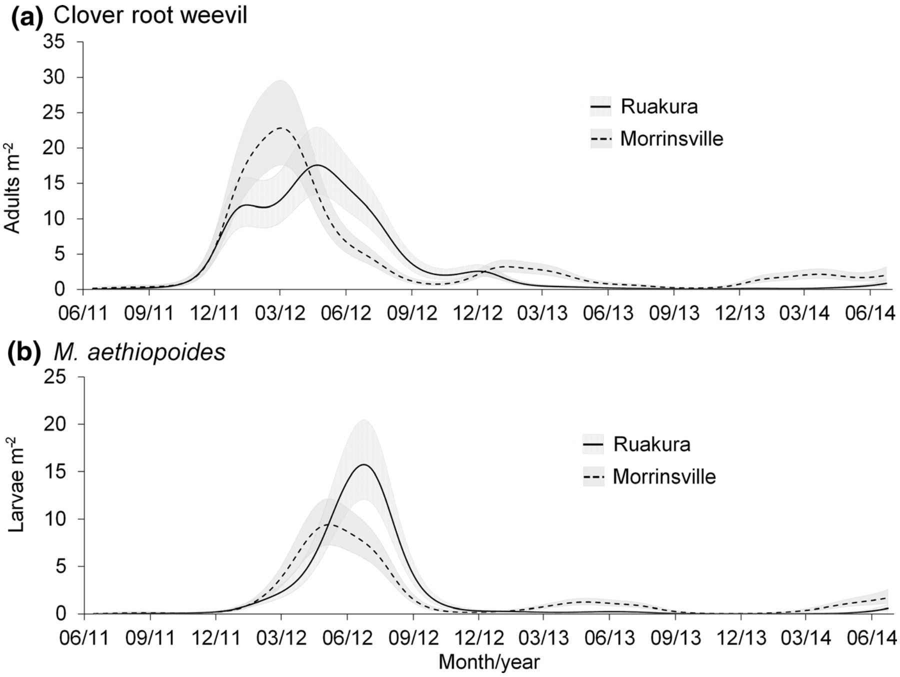


Fig. 1 Temporal trends derived from Bayesian analysis in the population abundance of **a** clover root weevil adults and **b** *Microctonus aethiopoides* larvae at Morrinsville and Ruakura from September 2011 to June 2014. Bands are 95% least significance interval bands between sites. The two sites are significantly different at the 5% level where they do not overlap. Note vertical scales differ

Microctonus aethiopoides larval abundance (Fig. 1b) was extremely low from September to January each year but built up to levels exceeding host densities in some winter samples due to the presence of multiple *M. aethiopoides* larvae in many hosts. Parasitised hosts had only one larvae per host from late spring and over summer, but winter averages ranged from a maximum 2.4 ± 0.13 larvae per host at Morrinsville in 2013 to a low of 1.5 ± 0.08 larvae per host at Morrinsville in 2012. This pattern is consistent with an extreme population depression or even a localised extinction of *M. aethiopoides* during the spring period of host scarcity and recovery when hosts were abundant.

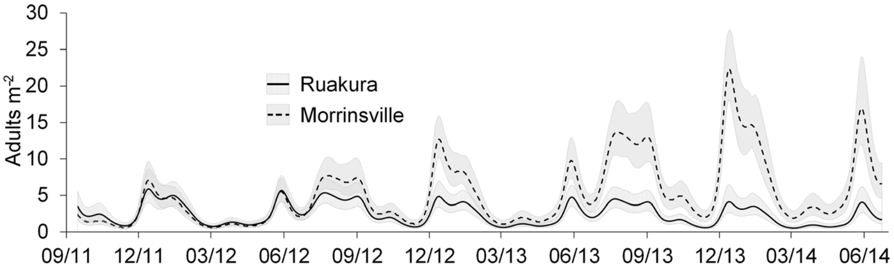
Overall, Argentine stem weevil adult populations were low. Although populations peaked at higher levels at Morrinsville than at Ruakura from December 2012 on, they only exceeded 15 m^{-2} in December 2013 (early summer) (Fig. 2a). At both sites, distinct peaks in weevil abundance associated with adult recruitment for generation 1 occurred in December/January and there was no evidence of a generation 2 peak in March. Instead, there was prolonged recruitment of Argentine stem weevil generation 3 adults commencing in May and peaking as late as July. Generations 1 and 3 had little overlap, with very low adult densities in October and November (spring) and again during February–April (late summer–autumn). The latter period of host scarcity was particularly strong in 2013 when no weevils were in samples collected at Morrinsville in February and Ruakura in March.

Figure 2b shows that, despite two protracted periods of host scarcity, *M. hyperodae* maintained relatively stable, albeit low, larval populations at Ruakura. Parasitoid larval populations very closely mirrored host populations with no evidence of a delayed density dependent response between the parasitoid and its host.

Seasonal patterns of percent parasitism

When parasitoid species are compared (Fig. 3), percent parasitism in generation 1 hosts (November–December) by *M. aethiopoides* was lower than *M. hyperodae,* albeit only significant for the pooled data in late 2011–early 2012. This aligns with the population data showing that, whereas *M. aethiopoides* experiences near extinction each spring, *M. hyperodae* bridges the spring period of host scarcity relatively successfully. In contrast, in the overwintering weevils

(a) Argentine stem weevil



(b) *M. hyperodae*

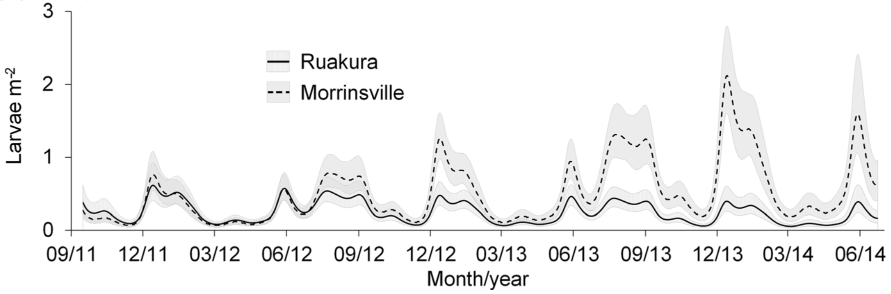


Fig. 2 Temporal trends derived from Bayesian analysis showing the mirroring population abundance of **a** Argentine stem weevil adults and **b** *Microctonus hyperodae* larvae at Morrinsville and Ruakura from September 2011 to June 2014. Bands are 95% least significance interval bands between sites. The two sites are significantly different at the 5% level where they do not overlap. Note vertical scales differ

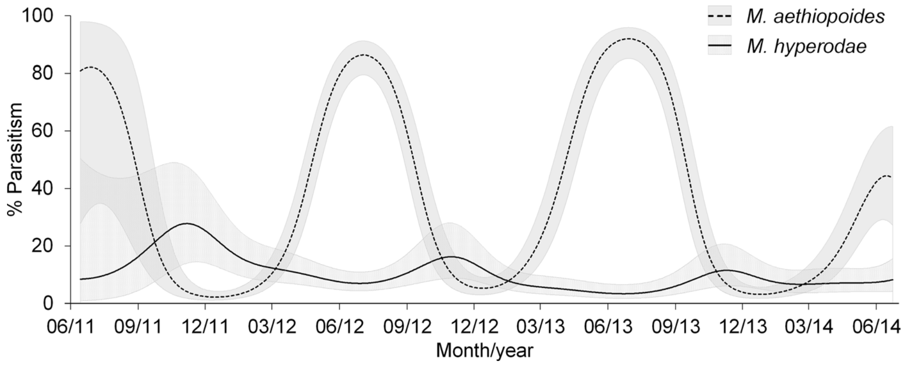


Fig. 3 Comparison of percent parasitism by *Microctonus aethiopoides* and *M. hyperodae*. Curves derived from Bayesian analysis. Bands are 95% least significance interval bands for comparing parasitism levels between weevil species. The percentages are different at the 5% level where the bands do not overlap

(May–August), percent parasitism by *M. hyperodae* was significantly lower than *M. aethiopoides* (Fig. 3). This aligns with the population data showing that whereas *M. aethiopoides* populations increased over summer, the lack of available hosts through late summer into early autumn led to a decrease in *M. hyperodae* populations (Fig. 2).

Comparison between 1990s and 2011–2014 Argentine stem weevil population and parasitism levels

Only the patterns of 1990s and 2011–2014 Argentine stem weevil population abundance data (Fig. 4) can be compared as different sampling methods were used. However, even allowing for the inefficiencies of suction sampling (McNeill and van Koten 2020), the 2011–2014 populations were very low. In 1993–1996, Argentine stem weevil generation 1 adults overlapped a large generation 2 (Fig. 4a). This resulted in increasing availability of hosts for *M. hyperodae* through summer from December to a peak in March/April. However, in 2011–2014, there was no discernible weevil generation 2 peak in March and a prolonged generation 3 recruitment peaking in July (Fig. 4b). The lack of generation 2 caused a three-month period of poor host availability for *M. hyperodae* over late summer and early autumn. The percent parasitism data shows *M. hyperodae* adults were active during this period.

Climate has changed over time between these two studies. Dry summers have become common. During the 1990s' study, the average total summer (December-February) rainfall at Ruakura was 227 ± 26 mm (minimum 181 mm) while during the current study 151 mm was recorded in 2012/2013 and 133 mm in 2013/2014 (CliFlo 2020). These summer droughts have a marked effect on pasture cover, e.g. in this study grass cover in summer at Ruakura declined to 20% or below in both 2013 and 2014. Mean summer temperatures at Ruakura (CliFlo 2020) have significantly increased since 1990 ($y = 0.046x - 74.2$, $R^2 = 0.17$, $P = 0.029$) with temperatures for the first five summers in the 1990s averaging 17.7 °C compared with 18.5 °C for the first five summers from 2010. Studies by Barker (1988) gave the estimate of 454 day-degrees (°D) above 10 °C for Argentine stem weevil to complete development. Theoretically this would have allowed four weevil generations in the 2012/2013 season and three generations in the remaining seasons. The weevil population data in this study are consistent with those predictions (Fig. 2a). With the Barlow et al. (1994) estimate of 386°D above 10 °C to complete development, *M. hyperodae* would complete three generations between October and March inclusive, with adults emerging in December, February, and March.

Discussion

This study shows that, although both *M. aethiopoides* and *M. hyperodae* have been successful introductions for the biocontrol of their target weevil pests, the efficacy of the latter in the Waikato region is hampered severely by asynchrony with its host (Fig. 4). The *M.*

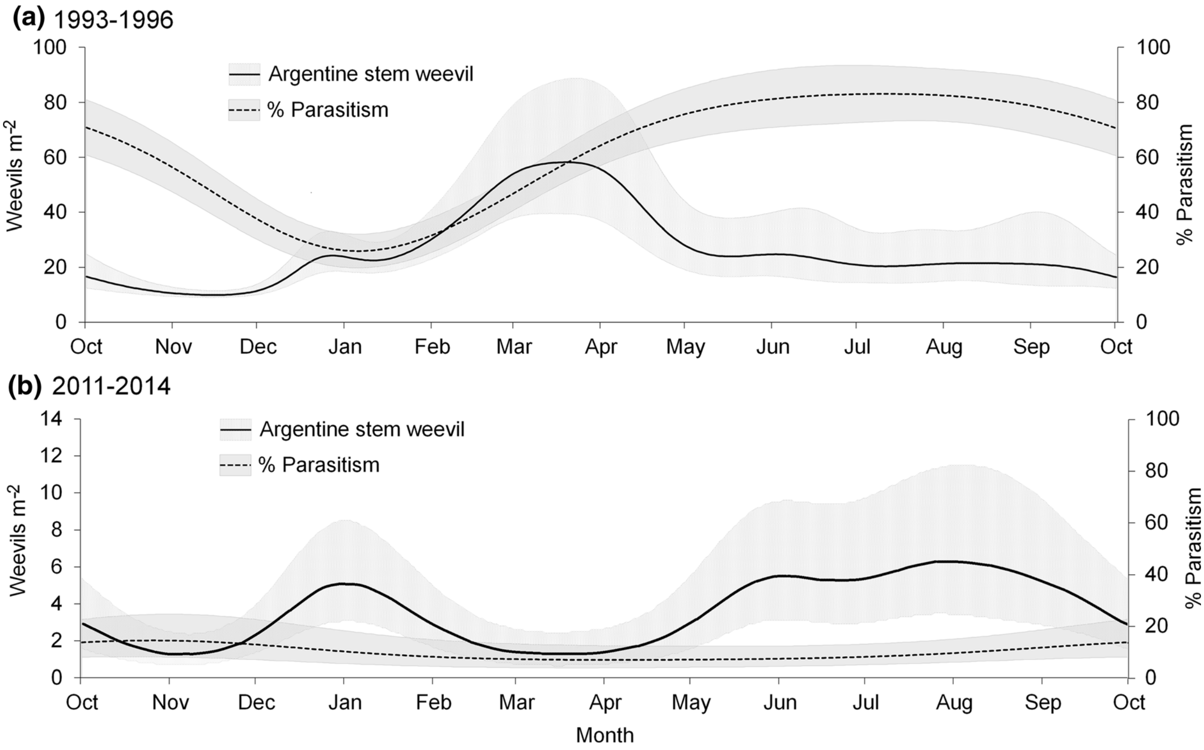


Fig. 4 Comparison of seasonal variation of Argentine stem weevil adult abundance and parasitism from **a** the Ruakura *M. hyperodae* release site 1993–1996 (Barker 2013) and **b** the pooled Morrinsville and Ruakura sites 2011–2014. Curves derived from Bayesian analysis. Bands are 5% least significance interval bands for testing differences between time points. Note vertical scales differ

aethiopoides-clover root weevil interaction demonstrates the importance of host availability over summer. The combination of very low parasitism and parasitoid larval densities from November to January indicates that the absence of clover root weevil adults during spring (September till November) causes near extinction of *M. aethiopoides* populations each year. Fortunately, with overlapping summer and autumn clover root weevil generations, *M. aethiopoides* has a constant supply of hosts when its generation time is shortest and by autumn the parasitoid reaches levels that give good control in generation 2 weevils.

The ability to recover from extremely low levels each spring allows *M. aethiopoides* parasitism levels and larval populations to follow the host populations in a typical predator–prey relationship. The parasitoid population levels were able to increase rapidly in response to a minor outbreak of clover root weevil over summer 2011/2012 (Fig. 1). This rapid increase was probably aided by the Irish strain of *M. aethiopoides* being facultatively gregarious (Gerard et al. 2007), which allows parasitoid larval density to persist at relatively high levels through times of low host availability. The resulting high parasitism levels in winter 2012 reduced the weevil populations back down to the very low levels recorded after the successful biocontrol releases in 2006 (Gerard et al. 2011). The low winter clover root weevil adult populations and *M. aethiopoides* larval populations were similar in both 2013 and 2014 and in the subsequent three years (unpublished data), thus may reflect the host-parasitoid equilibrium at these sites.

In comparison to *M. aethiopoides, M. hyperodae* has a shorter period of host unavailability in spring and builds up to higher populations (Fig. 2) and parasitism levels (Fig. 3) in its generation 1 hosts. However, in contrast to *M. aethiopoides*, due to the absence of a detectable Argentine stem weevil generation 2 in late summer/early autumn, *M. hyperodae* has a prolonged period of low host availability when its generation time is shortest. Furthermore, *M. hyperodae* seasonality is regulated by a photoperiod-induced diapause

(Goldson et al. 1993) so adults first appear in mid-November and are rarely found beyond mid-May (Phillips and Kean 2017). Inevitably, *M. hyperodae* populations and parasitism levels are relatively low in Argentine stem weevil generation 3 adults, the majority of which emerge from May onwards. Accordingly, *M. hyperodae* and Argentine stem weevil populations do not show the lags characteristic of predator–prey relationships. The very close mirroring of *M. hyperodae* abundance with that of Argentine stem weevil (Fig. 2) suggests the parasitoid was present and able to exploit its prey when it was available.

One major difference between the 1990s and 2011–2014 studies is that the former was on a *M. hyperodae* release site. It was known that Argentine stem weevil population density was dependant on the availability of favourable grass tillers per individual (Barker et al. 1989). Therefore, to ensure good host populations for the establishing parasitoid, pastures at the release sites had been sown with a low endophyte mix (*Lolium mutiflorum* Lam., (nil endophyte) L. and *L. perenne* L. (12% endophyte infection)) and the same mix was drilled into these pastures every autumn to maintain low endophyte levels in subsequent years (Barker and Addison 2006). In contrast, endophyte infection levels in the 2011–2014 study site pastures were high (≥ 94%), as typical in established Waikato pastures.

The endophyte *E. festucae* var. *lolii* confers resistance in ryegrass against Argentine stem weevil (Barker et al. 1983; Prestidge and Gallagher 1988; Prestidge et al. 1982) and its ability to prevent damage and reduce populations of this and other major pasture pests underlies the widespread use of this endophyte in pastoral agriculture in New Zealand (Caradus and Johnson 2020; Hume et al. 2020). Endophyte infection deters adult feeding and oviposition (Barker et al. 1984a) and lowers egg and larval survival (Barker et al 1984b). Peak alkaloid concentrations in ryegrass occur in summer/autumn (January–April) (Prestidge and Gallagher 1988; Finch et al. 2012; Thom et al. 2014). Therefore, while weevil oviposition can peak at moderate levels in spring in high endophyte pastures (though at lower levels than nil endophyte pastures), it declines rapidly in late spring/early summer and remains low into autumn (Popay and Mainland 1991; Popay et al. 1995). This proven efficacy of the endophytes in inhibiting Argentine stem weevil oviposition and larval development during summer is entirely consistent with the contrasting overall population levels between the 1990s' and 2011–2014 studies and the observed lack of generation 2 adults from February to April in the latter.

Even though endophyte infection alters Argentine stem weevil behaviour and therefore susceptibility to parasitism (Gerard 2000), it is unlikely to alter the number of generations of the parasitoid. No detrimental effect on *M. hyperodae* has been found with AR37 (Bultman et al. 2003), the recommended endophyte strain for the Waikato region (Popay and Thom 2009). While *M. hyperodae* larvae develop more slowly in weevils fed grasses infected with wild-type or AR1 endophyte strains relative to nil endophyte (Barker and Addison 1996; Bultman et al. 2003), there is no impact on the fitness of resultant adults (Urrutia et al. 2007). Therefore, the second and final parasitoid generation adults would emerge in late summer/early autumn at time of lowest host availability.

The second major difference between the 1990s and 2011–2014 studies are the impacts of climate. A partial Argentine stem weevil generation 3 in Waikato was observed in some years during the 1980s by Barker et al. (1989) and with a warming climate the previously published day-degree accumulation requirements (Barlow et al. 1994) and insect data presented are consistent with a late autumn weevil emergence now being the norm in Waikato. The increased temperatures and frequency of summer droughts are likely to intensify the effect of endophyte on Argentine stem weevil adult populations in the Waikato region. Levels of endophyte hyphae (di Menna and Waller 1986) and active alkaloids in the leaves deterring Argentine stem weevil (Ball et al. 1991; Hennessy et al. 2016) are highest when temperatures are warm. In addition, summer droughts in Waikato lead to increased pressure from black beetle *Heteronycus arator* (F.), which feeds on the same low endophyte pasture grasses favoured by the weevil (Bell et al. 2011). Under these conditions, overall grass cover decreases and amongst the surviving plants, endophyte-infected ryegrasses, especially those infected with AR37, retain relatively high tiller densities while those without endophyte have very low tiller densities (Thom et al. 2014).

Furthermore, as Argentine stem weevil is a rapid coloniser (Thom et al. 2014), it is possible that inward adult migration from roadsides and other areas with alternative host grasses may augment pasture populations once endophyte alkaloid levels had declined and seedlings of the favourable weed grass *Poa annua* established (Prestidge et al. 1989). As parasitized weevils lose the ability to develop flight muscles (Barker 2013), inward migration would dilute resident parasitism levels.

In conclusion, we deem that the large differences between 1990s and current levels of parasitism by *M. hyperodae* in overwintering Waikato Argentine stem weevil populations are most likely due to the combination of the expected endophyte-induced suppression of the weevil generation 2 at time of peak parasitoid activity and the occurrence of a third generation of adult weevils after most parasitoid adult activity has ceased, both of which would be enhanced by a warming climate and hot dry summers. This does not preclude the possibility that there has been a genetic shift in Argentine stem weevil to avoid parasitism (Harrop et al. 2020; Tomasetto et al. 2018b). However, while there is geographic genetic variation in New Zealand populations of *L. bonariensis,* to date no genetic association has been found with parasitism by *M. hyperodae* (Harrop et al. 2020). Also, the premise for this shift was based on a time series of overwintering percent parasitism data, where most initial 1991–1996 data, especially that from the North Island, were from parasitoid release sites sown with low endophyte grasses to ensure good Argentine stem weevil populations (Barker and Addison 2006; Goldson et al. 1998). Our study shows the importance of sampling host and parasitoid abundance throughout the year, and taking into consideration agricultural practices, when trying to determine what drives the success or apparent failure of a biocontrol agent.

This study has shown that *M. hyperodae* has remarkable persistence: it prevails despite very low host populations and inhospitable Waikato pastures to recover to close to 1990s' parasitism levels each spring. Farmers must use endophyte-infected ryegrasses to maintain pastures under the high pest pressure in the region. Therefore, to enable *M. hyperodae* populations to reach adequate levels to protect vulnerable grasses and prevent outbreaks of Argentine stem weevil, consideration needs to be given as to how to incorporate host-parasitoid refugia into farm systems that will enable the parasitoid populations to increase rather decline over summer. This would include pasture and roadside grasses that host yet tolerate the weevil.

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Declarations

Conflict of interest No conflicts of interest. Approval has been obtained from DairyNZ to publish.

Research involving animal participants Invertebrates not covered by animal ethics.

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