Bulletin of Entomological Research (2011) **101**, 295–303
doi:10.1017/S0007485310000507

First published online 21 December 2010

Argentine stem weevil (*Listronotus bonariensis*, Coleoptera: Curculionidae) population dynamics in Canterbury, New Zealand dryland pasture

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Abstract

The Argentine stem weevil (*Listronotus bonariensis*) was an economically important pest in New Zealand pastures until the release of the parasitoid *Microctonus hyperodae*. This contribution uses historical data to investigate the regulation of the pest populations prior to, and somewhat during, the establishment of this parasitoid in dryland Canterbury, New Zealand. Thus, a significant goal of this study is to provide an *L. bonariensis* population dynamics baseline for any future work that aims to analyse the full effects of *M. hyperodae* on the weevil, now that equilibrium with the weevil host has been reached.

The population dynamics of *L. bonariensis*, based on a life-table approach, were investigated using data collected regularly for eight years from populations in Canterbury, New Zealand. The key factor affecting end-of-season *L. bonariensis* density was found to be variation in second generation fourth instar prepupal and pupal mortality. This may have been caused by arrested development and ongoing mortality resulting from the onset of cooler autumnal conditions.

A compensatory response was found in recruitment to the second summer weevil generation, whereby the realised fecundity of the emergent first summer generation of weevils was found to be negatively related to the density of adult weevils per ryegrass tiller. This is the first time that this has been found via long-term population analysis of *L. bonariensis*, although indications of this have been found elsewhere in caging, pot and small plot experiments.

In this study, the effect of the parasitoid biocontrol agent *Microctonus hyperodae* on *L. bonariensis* population dynamics was unclear, as the analysis covered a period when the parasitoid *Microctonus hyperodae* was introduced and still establishing. It does, however, raise important questions for future analysis in terms of the interaction between parasitism and unrealised fecundity.

The results in this contribution also highlighted regional differences. Overwintering mortality of adult weevils in Canterbury was constant between years, whilst earlier studies in the North Island Waikato region indicated this mortality was density dependent. In addition, the availability of tillers in endophyte-free ryegrass pastures in Canterbury had no influence on egg and

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early-instar larval survival, which contrasts with the finding from endophytic Waikato pastures.

Keywords: life tables, mortality, density dependence

(Accepted 2 August 2010)

Introduction

Argentine stem weevil (*Listronotus bonariensis* (Kuschel), Coleoptera: Curculionidae) was the most serious pest of Graminae in New Zealand's improved pasture for more than 100 years. When uncontrolled, this species was estimated to cause losses to the pastoral sector of NZ$78–251M annually (e.g. Prestidge *et al*., 1991). The weevil has also been reported to cause sporadic problems elsewhere, usually in cereal crops. Gassen (1984) identified *L. bonariensis* as being damaging to wheat in southern Brazil. Similarly in Argentina, it has been noted that the weevil larvae feed on wheat shoots and buds resulting in shoot mortality, reduction in shoot numbers and reduced yields (Anonymous, 1996). *Listronotus bonariensis* is also established in Australia, where it was first noted as a problem in sports turf (Hardy *et al*., 1979).

The life history of *L. bonariensis*, as reflected in fig. 1, is well known and includes the occurrence of reproductive diapause and dispersive flights (e.g. Pottinger, 1961; Goldson, 1981; Goldson *et al*., 1998a, 1999). In brief, the weevil is bivoltine, with first generation egg-laying commencing in late September following the cessation of weevil overwintering diapause. Eggs are laid in the sheaths of the grass tillers, and the resulting larvae develop through four larval instars, destroying 3–5 tillers in the process (Prestidge *et al*., 1984). In addition, about 30% of the total larvae have also been found to develop in the pasture thatch (Goldson *et al*., 2001). Mature fourth instar/prepupal larvae cease feeding and move into the soil where they pupate in earthen cells. First generation adult eclosion begins in early December and peaks in early January. A second larval generation develops over the summer with second generation teneral adults appearing in early March with eclosion continuing well into the winter, ending in mid-June. This second generation of adults, along with some surviving first generation adults, overwinter in a state of reproductive diapause triggered by critical photoperiod. These weevils form the basis of the next season's spring reproductive population.

Resistance to weevil attack occurs when perennial ryegrass plants are infected with the endophyte *Neotyphodium lolii* (Latch Christensen and Samuels) (formerly *Acremonium lolii*) (Ascomycota Clavicipitaceae). Such infection deters oviposition and makes the tillers toxic to larvae (Prestidge *et al*., 1982). The use of *N. lolii* has become an important component of New Zealand's pasture pest management (Easton, 2007).

The severe economic impact of *L. bonariensis* led to the 1991 release of the South American thelykotous, koinobiont endoparasitoid wasp, *Microctonus hyperodae* Loan (Hymenoptera: Braconidae), as a control against *L. bonariensis* (Goldson *et al*., 1993). This wasp parasitises the adult weevils and almost immediately causes sterilisation; thereafter, the four larval instars develop within the still-live weevil. Host weevil mortality occurs at the time of fourth instar (prepupal) emergence. The parasitoid was found to establish rapidly throughout New Zealand, often resulting in peak host parasitism levels of as much as 80% (e.g. Goldson *et al*., 1994).

Barker *et al*. (1989) have described *L. bonariensis* population dynamics prior to parasitoid release in comparatively warm and wet North Island Waikato dairy pastures (*ca*. 37.78°S, 175.35°E), which consist mainly of endophytic perennial ryegrass *Lolium perenne* L. plants (cultivar Grasslands Nui) and white clover *Trifolium repens* L. These workers showed that under such circumstances the weevil population regulatory processes primarily resulted from density dependent mortality of overwintering adult weevils, ovipositional competition for endophyte-free tiller resources and tiller resource competition between early-instars.

In contrast to the North Island Waikato region, while there have been some basic bionomic studies in dryland non-endophytic sheep pasture *Lolium multiflorum* × *perenne* L. (cultivar Grasslands Manawa) in Canterbury (Goldson *et al*., 1998a), there has been no comprehensive baseline population dynamics analysis studies of *L. bonariensis*. Consequently, to address this absence of information and as part of the overall biological control programme, weevil populations at Lincoln, Canterbury (*ca*. 43.64°S, 172.47°E) were monitored continuously over eight consecutive years. Such work is of significance because it was conducted in a dryland ecosystem, typical of where *L. bonariensis* can be particularly damaging (e.g. Goldson & Trought, 1980).

Based on the monitoring work, this contribution therefore uses historical data to investigate the regulation of the weevil pest populations prior to, and somewhat during, the establishment of the parasitoid in Canterbury dryland conditions. Thus, a significant goal of this study is to provide an *L. bonariensis* population dynamics baseline for any future work that aims to analyse the full effects of *M. hyperodae* on the weevil, now that equilibrium with the weevil host has been reached.

Materials and methods

Study site and sampling of weevil populations

Egg, larval and adult stages of *L. bonariensis* were sampled regularly from 26 November 1990 to 15 February 1999 at the AgResearch Farm at Lincoln. The paddock was first sown in autumn 1988 with a mixture of cv. Manawa ryegrass and white clover and was periodically renovated to maintain sward quality. This paddock was the site of the original *M. hyperodae* releases in the winter of 1991 (Goldson *et al*., 1993). Sampling of all stages of *L. bonariensis* occurred approximately fortnightly from spring to autumn and approximately monthly during the winter. The sampling techniques used are described in detail elsewhere (Goldson *et al*., 1998a); but, briefly, eggs were sampled by inspection of ryegrass tillers, larvae by heat extraction from ryegrass tillers and adults by flotation extraction from 450 mm × 40 mm × 80 mm deep turf

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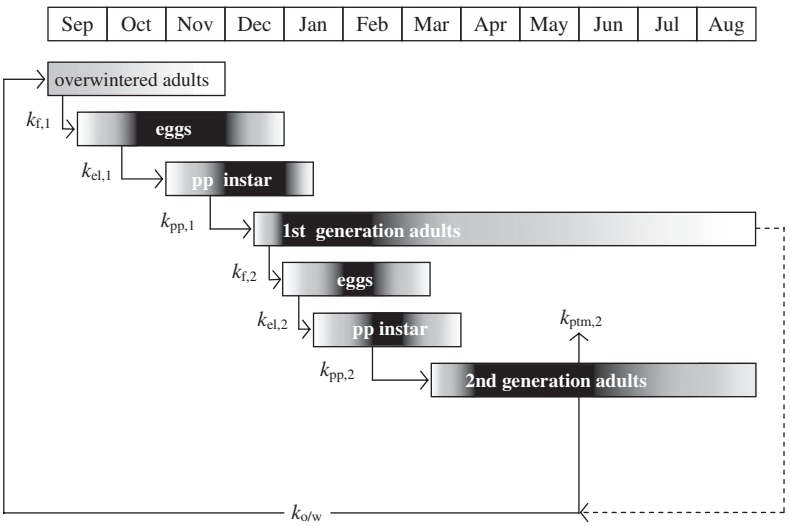

Fig. 1. Diagram showing the timing of, and estimated mortalities of *L. bonariensis* life stages used in this analysis. Shading of the life stages indicates relative abundance, with the darkest shading indicating peaks in abundance. Mortality rates are expressed as *k*-values where: $k_{f,1}$ and $k_{f,2}$ = unrealized fecundity in the founding of the first and second generations per season respectively; $k_{el,1}$ and $k_{el,2}$ = mortality of the egg and early instar larval stages in the first and second generations respectively; $k_{pp,1}$ and $k_{pp,2}$ = mortality of the fourth (i.e. fourth instar/prepupal and pupal) stages in the first and second generations respectively; k_{ptm2} = parasitism of second generation adults by *M. hyperodae*; and *k*o/w = overwintering mortality. The dashed line indicates that some of the late-emerging (February) first generation adults go directly into reproductive diapause and contribute to the overwintering adult generation (Goldson, 1981).

pasture samples. The latter were taken from each of five designated blocks in the research paddock, and the number of turves taken per block varied from four to ten to maintain a standard error of the mean of ≤20% (Goldson *et al.*, 1998a).

Life table preparation

Partial life tables (table 1) were constructed for the *L. bonariensis* populations monitored at Lincoln between late 1990 to early 1998. Figure 1 illustrates the phenology of the weevil population and defines the transitional mortality factors that were estimated in this analysis. The life tables were not entirely complete because two factors were not quantified. The first of these is the possibility of redistribution arising from trivial weevil flight (e.g. Goldson, 1981; Goldson *et al.*, 1999). However, in established pasture, this effect is likely to be minor given that incoming weevils (from surrounding areas) were likely to have arrived in similar numbers to those leaving (Goldson, 1981; Goldson *et al.*, 1999). Should any dispersive losses have occurred, they would have been included in the unrealised fecundity 'mortality' factor in the first and second summer generations ($k_{f,1}$, $k_{f,2}$), since flights can coincide with the times that overwintered (spring) and first summer generation adults are reproducing (fig. 1) (Goldson *et al.*, 1999). The second factor is the contribution of *M. hyperodae* parasitism to unrealised fecundity of first generation adults, since parasitised weevils are not reproductive (Goldson *et al.*, 1998a,b). It is notable, however, that, at least in the first phases of this study, parasitism levels were relatively low, as at that time the parasitoid populations were still building. Thus, taken across the whole study period, this influence would have been relatively minor (Goldson *et al.*, 1998b). Nonetheless, these two factors need to be considered when interpreting the results.

The number of individuals entering the egg, prepupal and teneral adult stages were estimated using the graphical integration method of Southwood and Jepson (Southwood, 1978). For the egg and larval stages, the calculations were made using physiological time; where successive estimates of stage densities, obtained through sampling, were plotted against cumulative degree-days and the area under the resulting curve was divided by the mean duration (in degree-days) of the stage. The degree-day requirements and threshold temperatures for development used in these estimations were: 72.6 degree-days above 11.9°C for the egg stage to the prepupal stage and 33.6 degree-days above 12.2°C for the prepual stage to adult stage (Kalvelage, 1999). In this study, the term 'prepupal' was taken to include the fourth instar as it is this stage that exits the tillers pending pupation. Meteorological data were recorded by a weather station located approximately 500 m from the study site. Temperatures were assumed to vary sinusoidally through the 24-h day and the number of degree-days accumulated per day was calculated using the trapezium method (Barlow & Dixon, 1980): degree-days per day = $0.25((T_{max}–T_h)+(T_{min}–T_h)+2(T_{mean}–T_h))$ where T_{max}, T_{min} and T_{mean} are the maximum, minimum and mean daily temperatures, respectively, and T_h is the threshold temperature for development for the stage.

Prepupae were chosen as the best estimate of larval density because they are relatively large and unlikely to be overlooked in tiller samples; they also have a relatively high survival rate and were unlikely to bias the estimates of stage recruitment. Also, their relatively long stage duration reduced the chances of them being missed between sampling dates. Prepupal densities were multiplied by 1.54 to correct for sampling bias arising from larval development in the thatch (Goldson *et al.*, 2001).

The appearance of teneral adults was used to estimate recruitment to the adult stage; the teneral stage was assumed

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Table 1. Stage-specific mortality rates for *L. bonariensis* populations at Lincoln (1990–1998).

Year	$k_{f,1}$	$k_{el,1}$	$k_{pp,1}$	$k_{f,2}$	$k_{el,2}$	$k_{pp,2}$	$k_{ptm,2}$	$k_{o/w}$	K
1990/91	0.636	−0.029	1.371	1.107	0.814	1.945	0.033	0.370	6.248
1991/92	1.153	0.434	−0.051	–	–	1.219	0.037	0.298	5.798
1992/93	0.894	0.148	0.591	1.384	0.791	0.448	0.255	0.371	4.882
1993/94	0.907	0.488	0.500	1.192	−0.272	1.875	0.316	0.363	5.368
1994/95	0.591	0.879	0.411	0.511	0.095	1.155	0.595	0.091	4.327
1995/96	1.164	0.322	0.444	1.359	0.488	1.957	0.484	0.308	6.526
1996/97	0.869	0.931	0.051	1.318	0.170	1.063	0.201	0.383	4.986
1997/98	1.003	0.219	0.865	0.872	−0.006	1.297	–	–	4.251

Refer to figure 1 caption for stage mortality definitions.

to last for approximately 14 days, based on laboratory observations (Pottinger, 1961). Again, densities were estimated using the graphical integration method of Southwood and Jepson (Southwood, 1978).

Eight full seasons of data were available, but some data were omitted because of known sampling errors. In the 1991/92 season, no second generation eggs were detected from the tiller samples, yet larvae were subsequently found, indicating sampling deficiency rather than absence. To remedy this, the second generation egg density for this season was set to be the same as the maximum potential fecundity, which meant that unrealised fecundity was underestimated and egg to prepupal mortality was overestimated. However, assuming that the larval density estimates were accurate, total seasonal mortality would remain unaffected. It was, therefore, necessary that the estimates for second generation 1991/92 eggs and larvae be omitted. In the 1997/98 season, no estimates were made of adult density in early winter, with the last sample taken on 2 March 1998. Because recruitment of second generation adults continues after this time until early June (Goldson *et al.*, 1998a), parasitism of second generation adults, overwintering mortality and, therefore, total seasonal mortality could not be estimated for 1997/98.

Key factor analysis

To compare the variation in mortality rates between stages and years, k-values were calculated as $k = \log$ (number entering stage)–log (number surviving to next stage), except where noted below. The unrealised fecundity k-values ($k_{f,1}$ and $k_{f,2}$) were estimated from the difference between the maximum potential fecundity of the weevil population present and the observed number of eggs laid. For the egg laying that founded the first generation, maximum potential fecundity was calculated by multiplying the peak number of overwintered fecund females by the species' mean fecundity of 320 eggs (Malone, 1987). For the egg laying that founded the second summer generation, maximum potential fecundity was calculated by dividing the number of teneral weevils by two (i.e. assuming a 50:50 sex ratio, (Goldson, 1979)) and multiplying this figure by mean female fecundity.

Overwintering mortality (k_{ow}) was calculated as the logarithm of the (unparasitised) adult density in June minus the logarithm of the (unparasitised) adult density in late August/early September when the weevils come out of reproductive diapause.

Total seasonal mortality (K) was calculated as the sum of the individual stage k-values. The mortality contributing most to the total seasonal variation in mortality (i.e. the key factor) was assessed by visual comparison of the variation in k-values with K (Varley & Gradwell, 1960) and by regression of the k-values on K (Podoler & Rogers, 1975).

Manly key factor analysis

In addition to the Varley & Gradwell (1960) method and Podoler & Rogers' (1975) method of key-factor analysis described above, the method of Manly (1977) was also used on the reduced data set (1991/92 and 1997/98 seasons excluded). This has the advantage that it takes into account the order in which the mortality factors operate, so that any damping of variation due to density dependence in earlier stages is accounted for in the analysis of the following stages. Unlike the earlier methods, which identify the life stage that mainly accounts for changes in total mortality, Manly's method identifies the most influential life stages causing population change and may recognise key factors which are unclear in other analyses (Manly, 1977). The contribution of the variation in mortality in stage i to the variation in numbers entering the final stage n was estimated as:

$$A_i = \mathrm{var}(\varepsilon_i) \prod_{j=i+1}^{n-1} (1-\delta)_j^2 \qquad (1)$$

where δ is the slope and var(ε) is the residual mean square estimated from the linear regression of stage k versus log (stage density). Ordinary least-squares regression was used except that the residual mean square was estimated as the mean square divided by the number of seasons–1 (S–1), rather than the usual S–2 (Manly, 1990). Variation in the number of fecund females at the start of each season, A_0, was also included as a source of variation because the omission of the 1991/92 and 1997/98 seasons, and spring dispersal meant that the numbers at the start of each season were unrelated from one season to the next. The variance A_0 was calculated as above, except that var(ε) was replaced with the variance in fecund female density at the start of each season. The stage A_i values were summed to give the variation in the numbers entering the final stage, var (R_9), which in this case was variation in the density of adults at the end of the winter diapause. The key factor is the stage whose weighted variation, A_i, contributes most to the total variation, usually expressed as a percentage of var(R_9).

Considering that different factors play different roles in population dynamics, key factor analysis has some limitation in repeatedly determining the true key factor (if any) without fail (Royama, 1996). However, by combining the results from the different key factor analytical methods described in this study, it is likely that the correct candidate factors were identified making such information useful for future investigation.

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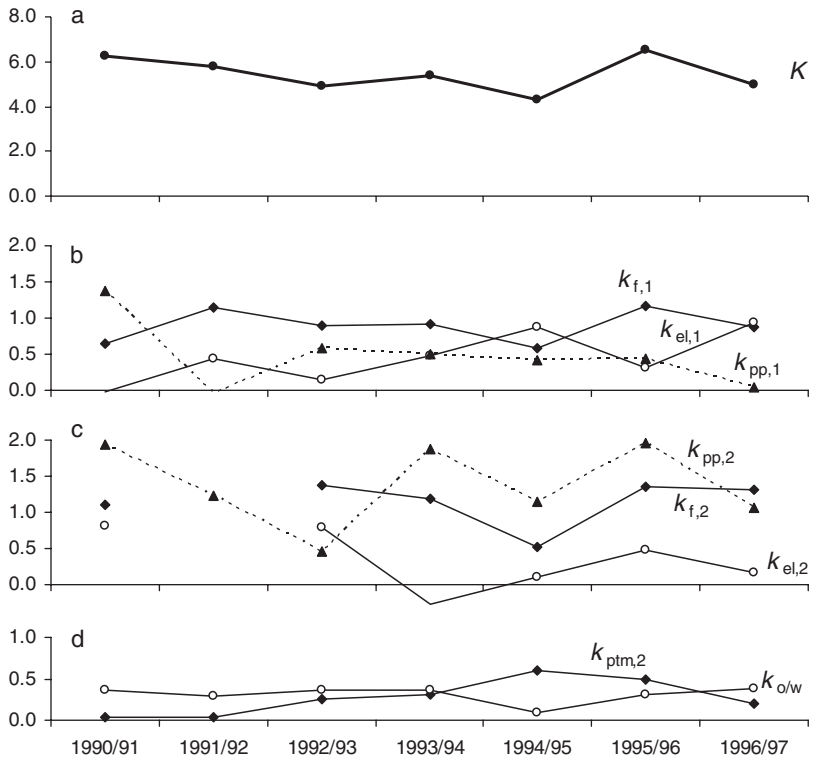

Fig. 2. *k*-factor analysis of *Listronotus bonariensis* at Lincoln, 1990–97. Refer to fig. 1 caption for stage mortality definitions.

Density relationships

Density-dependent mortality factors were assessed by regressing estimated *k*-values against the logarithm of the stage densities (per m^2) on which they acted; a positive slope is indicative of direct density dependence (Southwood, 1978). However, because $\log(N_t)$ appears in both the x and y variables, such regressions can produce a spurious result due to sampling error (Southwood, 1978). Therefore, another test for density dependence, the functional regression (Smith, 1973), was also used. This method calculates the functional relationship between the density of successive stages ($\log(N_{t+1})$ vs $\log(N_t)$), based on the assumption that the sampling errors in $\log(N_{t+1})$ and $\log(N_t)$ will be similar. A functional regression coefficient (slope) that is significantly less than one suggests direct density dependence. The *k*-value regression tests were repeated using the ratio of the stage densities to tiller densities as $\log(N_t/100$ tillers) to investigate the effect of tiller availability on population regulation.

In addition, to ensure that the obtained density relationship is not attributed to a 'spurious regression', the Augmented Dickey-Fuller (ADF) test was conducted. Granger & Newbold (1974) first introduced the notion of a 'spurious regression', which they argued produces statistically significant results between two non-stationary random-walk time series (i.e. two random time series plotted one against the other contain a trend). The ADF test assesses if each density is a non-stationary random-walk. The idea of a 'spurious regression' only becomes an issue if both densities in a regression are assessed as consisting of potentially non-stationary random-walk series.

Climate relationships

Relationships of *k*-values to six abiotic and resource variables were also tested. These were rainfall (mm), maximum and mean air temperatures (°C), minimum grass temperatures (°C) and number of ground frosts and average tiller density (tillers m^{-2}). The tiller density and temperature variables affecting each life stage grouping were calculated as three-monthly means encompassing the month of peak abundance of the stage being tested and one month either side. Rainfall and frost were summed over the same periods. Stepwise linear regression was used to model each *k*-value against the logarithm of the early stage density on which it acts, as well as each of the six weather and resource variables.

Results

Key factors

Variation in the mortality of second summer generation fourth instar/prepupal larvae and pupae $k_{pp,2}$ most closely followed variation in total mortality K (table 1, fig. 2). Regression of *k*-values on K confirmed $k_{pp,2}$ as the key factor, as this gave a slope closest to unity, with a nearly significant 41% of the variation in R_9 explained by K (linear regression: $k_{pp,2} = -0.75 + 0.400\,K$, $R^2 = 0.41$, $P = 0.088$). No secondary key factors were identified either visually or by regression although visually $k_{f,1}$ could be interpreted as having an effect.

Manly's (1977) key factor analysis also identified $k_{pp,2}$ as the key factor, explaining 48% of the total variation in R_9 (table 2). The next largest contributor to total variation was

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Table 2. Summary of Manly's key factor analysis for *L. bonariensis* populations at Lincoln over six summer seasons ($S=6$). A_i = variation in stage mortalities weighted by subsequent density dependence (equation 1) and var(R_9) = variation in the number of weevils entering the final stage.

Stage mortality (i)	Percent contribution of A_i to var(R_9)	Percent change in var(R_9) if $A_i=0$
0 = number entering first stage	0.0	0.0
$1=k_{f,1}$	0.1	0.1
$2=k_{el,1}$	0.1	−0.2
$3=k_{pp,1}$	0.8	1.5
$4=k_{f,2}$	16.9	10.8
$5=k_{el,2}$	24.0	−34.1
$6=k_{pp,2}$	47.7	−52.9
$7=k_{ptm,2}$	7.3	90.7
$8=k_{o/w}$	3.1	−8.8

second generation egg and early larval instar mortality $k_{el,2}$. The importance of these two factors was confirmed by making them constant, which led to a 53% and 34% reduction, respectively, in the variation in R_9 (table 2). Variation in the number of fecund females at the start of each season did not contribute to the variation in the number of adults at the end of the season (table 2). The result from Podoler & Rogers' (1975) method on the reduced dataset also identified $k_{pp,2}$ as the key factor (table 3), although the second largest contributor in this method was first generation egg and early larval instar mortality $k_{el,1}$ as opposed to $k_{el,2}$.

Relationships with density and climate variables

Unrealised fecundity in first generation adults, $k_{f,2}$, showed a positive relationship with density, indicating density dependence (linear regression: $k_{f,2}=-0.319+0.764\log(N_t)$, $R^2=0.49$, df = 5, $P=0.048$; fig. 3b); this relationship was improved by expressing density relative to tiller availability (linear regression: $k_{f,2}=0.887+0.809\log(N_t/100$ tillers), $R^2=0.76$, df = 5, $P=0.007$). Using stepwise multiple regression, the influence of teneral weevil numbers and tiller density were found to be significant, with tiller density having a negative effect on unrealised fecundity whereas teneral density has a positive effect ($k_{f,2}=0.192$–0.000136 tillers $+0.843\log(N_t)$, $R^2=0.81$, df = 4, $P=0.016$). The functional regression test confirmed the direct density dependence in $k_{f,2}$ ($b=0.390$, $t=2.14$, df = 5, $P=0.043$), and the Manly key factor analysis suggested that this had the potential to regulate the population since removing the effect of this factor (by making it constant across seasons) led to an 11% increase in the variance of adult weevil density at the end of winter diapauses (table 2).

First generation prepupal stage ($k_{pp,1}$) mortality was positively related to density (linear regression: $k_{pp,1}=-1.42+0.803\log(N_t)$, $R^2=0.50$, df = 6, $P=0.031$, fig. 3a; functional regression coefficient $b=0.369$, $t=2.29$, df = 6, $P=0.031$), suggesting direct density dependence in this stage. The relationship was improved slightly by expressing density in relation to tillers (linear regression: $k_{pp,1}=-0.045+0.808\log(N_t/100$ tillers), $R^2=0.55$, df = 6, $P=0.021$).

In the stepwise regression, however, tiller density was not significant, whereas larval density and maximum air temperature both showed positive influences on this mortality rate ($k_{pp,1}=-5.55+0.843\log(N_t)+0.200$ Max temp, $R^2=0.83$, df = 5, $P=0.005$). Although $k_{pp,1}$ was identified as being potentially density dependent using classical methods, the Manly key factor analysis suggested that this factor would have limited regulatory potential because if it was made constant there was little change in the variance of the number of weevils entering the final stage (table 2).

Table 3. Summary of Podoler & Rogers' (1975) key factor analysis for *L. bonariensis* populations at Lincoln over six summer seasons ($S=6$).

Stage mortality (i)	Regression coefficient
$1=k_{f,1}$	0.116
$2=k_{el,1}$	−0.294
$3=k_{pp,1}$	0.255
$4=k_{f,2}$	0.194
$5=k_{el,2}$	0.192
$6=k_{pp,2}$	0.551
$7=k_{ptm,2}$	−0.076
$8=k_{o/w}$	0.062
sum	1.000

The Manly key factor analysis identified the factor with the greatest potential to regulate *L. bonariensis* populations as parasitism of second generation adults $k_{ptm,2}$, since variation in adult density at the end of the season was predicted to increase by 90.7% if $k_{ptm,2}$ was held constant (table 2). However, this result is very likely to be an artefact of the increasing levels of parasitism by *M. hyperodae* that occurred during the study. Figure 2c shows $k_{ptm,2}$ values plotted against host density with the two lowest k-values (circled) occurring in the 1990/91 and 1991/92 seasons when the parasitoid was in its earliest establishment phases. These data increased the slope of the regression and led to an overestimation of the importance of $k_{ptm,2}$ in modifying the variation in the earlier stages.

Mortality of first generation egg and early instar larvae $k_{el,1}$ showed a negative relationship with minimum grass temperature ($k_{el,1}=2.89$–0.611 Grass min temp, $R^2=0.53$, df = 6, $P=0.034$), suggesting that cool spring conditions may hamper the survival of these early stages. Overwintering mortality showed no variation with density, and was constant at around 55% ($k_{o/w}\approx 0.35$), except in the winter of 1995 when it was lower than usual (fig. 2d).

The results from the ADF tests indicated that none of the results presented above were attributed to a spurious regression.

Discussion

The results from this Canterbury dryland study indicate considerable divergence from the results gained from similar work in wetter and warmer Waikato dairy pastures (e.g. Barker *et al.*, 1989).

Key sources of mortality

In this study, second generation fourth instar mortality ($k_{pp,2}$) (fig. 2, table 3) was identified as the key mortality factor. The reason for this mortality being so important for determining the densities of subsequent generations is not immediately apparent. However, these high mortality rates did coincide with the onset of autumnal conditions. The cooler weather could have arrested fourth instar/pupal development sufficiently for substantial mortality to have occurred during their resulting protracted developmental period. To this effect,

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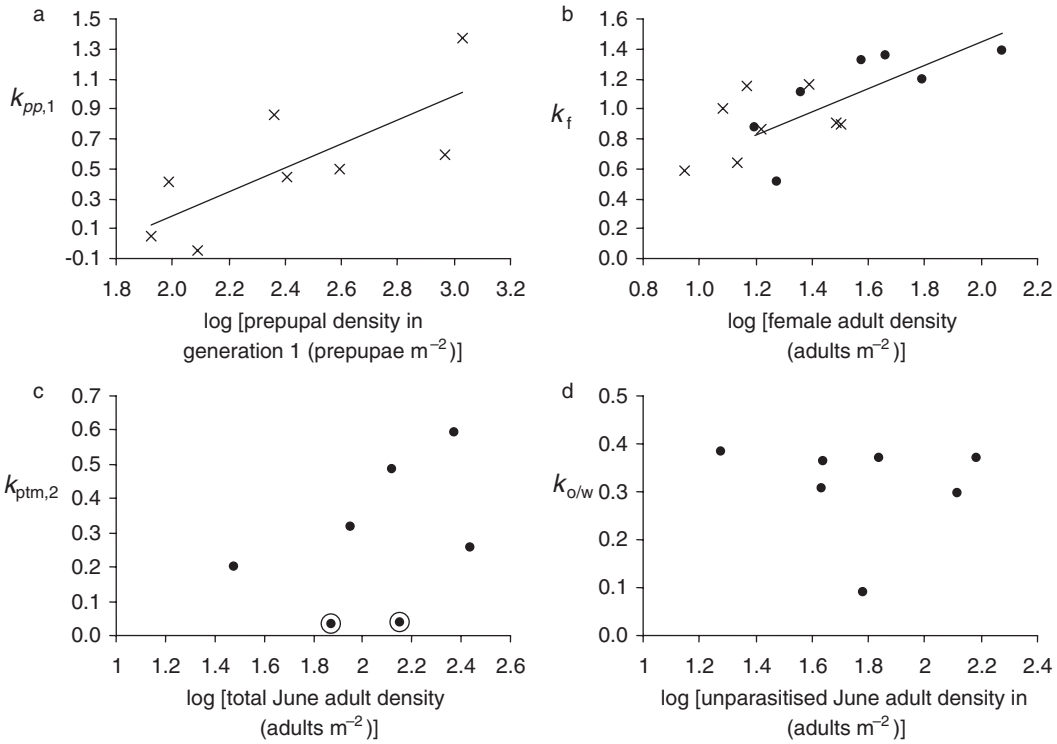

Fig. 3. Relationship of stage mortalities (expressed as *k*-values) with stage density. The data points circled in panel (c) are from 1990/91 and 1991/92 when the parasitoid *M. hyperodae* was not fully established. The *k*-value abbreviations are as in fig. 1 (×, 1st gen.; ●, 2nd gen.)

it is notable that adult eclosion commences in early March and continues in low numbers until late June (Goldson *et al*., 1998a).

Although much smaller in terms of absolute mortality, the analysis suggested that another key contributor to total variation in mortality was second generation egg and early larval instar mortality $k_{el,2}$ (table 2). This is consistent with the findings of Goldson (1979, 1982), who found high mortality rates between the egg and larval stages relating to the need for the neonate first instars to burrow into the tillers before they desiccate. Once established, Goldson (1979, 1982) found that larval mortality rates were thereafter low. It is, therefore, reasonable to assume that most of the mortality measured in this study occurred between the egg and first stage. In general, Goldson (1982) found that this mortality was higher in the tougher tillers of *L. perenne* than *L. multiflorum*.

Density dependence

Unrealised fecundity

A major component of the unrealised fecundity observed in the overwintered populations ($k_{f,1}$; fig. 1) was probably due to senescent overwintered female populations dying before laying their full egg complements. Similarly, unrealised fecundity observed in the first summer generation of weevils ($k_{f,2}$) (fig. 3b) was probably largely caused by the onset of photoperiodically induced diapause in early March, again before they could lay their full complement of eggs (Goldson, 1981; Goldson *et al*., 1998a).

It is of interest that this loss of fecundity was density dependent. A significant positive relationship was found between density of the first summer generation weevil population and unrealised fecundity ($k_{f,2}$) (fig. 3b). Likewise, a similar pattern was observed in the overwintered population between weevil density and unrealised fecundity ($k_{f,1}$) (fig. 3b). Higher tiller densities tended to offset these unrealised fecundity effects.

It is possible that these field-recognisable density dependent effects were due to a spacing pheromone. In caged conditions, Goldson (1981) found particularly strong evidence of ovipositional cessation and concomitant oocyte resorption. Barker *et al*. (1989), using potted ryegrass, also noted that *L. bonariensis* populations reduced per capita egg laying at high adult weevil densities. Similar experiments were conducted by Pilkington & Springett (1988), who suggested that the mechanism may be pheromonal. These workers noted that the proportion of weevil ovipositional holes plugged with frass increased with increasing weevil density and suggested that the pheromone was associated with the frass. Conversely, though, Barker *et al*. (1989) observed the opposite. Closer to the field environment, McNeill *et al*. (1998) used weevils confined in field plots and again found strong evidence for negative density dependent effects on egg-laying. That Prestidge *et al*. (1987) found a maximum of 3% multiple ovipositions per tiller and Barker *et al*. (1989) 6%, tends to support the Pilkington & Springett (1988) theory. Moreover, that tiller numbers were found to offset unrealised fecundity could well be the result of dilution of the effect of spacing pheromone, particularly if the effect is associated with the frequency of plugged (or unplugged) ovipositional holes.

Further work is required to clarify understanding of the changes in *L. bonariensis* oviposition behaviour and/or reproductive physiology as influenced by weevil density under

https://doi.org/10.1017/S0007485310000507 Published online by Cambridge University Press

field conditions. In terms of *M. hyperodae* biological control impact, interesting questions remain as to whether reduction in potential fecundity is in response to total adult weevils m^{-2} or just the unparasitised portion of the population. Should the latter apply, then potential population suppression through parasitoid-induced sterilisation and mortality of adult weevils could well be compensated for by increased reproductive effort by the unparasitised portion of the population. These questions are important subjects for future parasitoid impact analyses.

Egg to fourth instar mortality

The lack of any resource-based regulation of survival between the eggs to fourth instar stages in both generations ($k_{el,1}$ and $k_{el,2}$) in pasture with high densities of endophyte-free tillers (*ca*. 7000 m^{-2}) (Goldson *et al*., 1998a) is to be expected. This is in marked contrast to Barker *et al*.'s (1989) Waikato study, which had far fewer endophyte-free tillers (< 4000 m^{-2}).

In their Canterbury survey, McNeill *et al*. (2003) observed that even in *Lolium perenne* pasture with far lower numbers of endophyte-free tillers m^{-2} than in this study, they did not always exert population regulation. McNeill *et al*. (2003) concluded that the effects of tiller resource limitation only became apparent when there were high weevil populations, reflecting some kind of non-linear density-dependent response. The Canterbury results, therefore, contrast with the Waikato finding of Barker *et al*. (1989) who found clear population regulation in varyingly endophytic dairy pasture with tiller densities of around *ca*. 4200 tillers m^{-2} (Barker *et al*., 1984, 1986).

In general, the results in this study and those of Barker *et al*. (1989) highlight the importance of pasture type and climate in *L. bonariensis* population regulation.

Density-dependent fourth instar mortality

First generation pre-pupal instar ($k_{pp,1}$) (and pupal) mortality was positively related to density. This is difficult to explain as this mortality occurred at a time when pre-pupal fourth instar larvae had ceased to feed and emerge from the grass tillers before pupating in earthen cells. There is no evidence to suggest epizootics were the mechanism (Goldson, unpublished data). Moreover, although it was found that the relationship was improved slightly by expressing density in relation to tillers, it is most unlikely that resource limitation was an influence given that the cv. Manawa sheep pasture consisted of high densities of endophyte-free tillers (Goldson *et al*., 1998a). It is possible, however, that this density dependent effect was an artefact of the analytical method used. Although $k_{pp,1}$ was identified as being potentially density dependent using Varley & Gradwell's (1960) method, the Manly key factor analysis suggested that this factor would have had limited regulatory potential (table 2). It is also significant that prepupal stage mortality was not related to density in the second generation ($k_{pp,2}$) when larval densities were often higher and tiller densities were lower relative to those experienced by the first generation.

Overwintering mortality

Unlike populations from the Waikato (Barker *et al*., 1989), *L. bonariensis* adults in Canterbury showed no evidence of any density dependent overwintering mortality. In fact, overwintering mortality was remarkably constant and relatively low at *ca*. 55%, compared to 85–96% measured in the Waikato (Barker & Pottinger, 1982; Barker *et al*., 1989). This tends to confirm the relative importance of disease between the two regions. The effect of these differences in overwintering mortality is apparent when considering the relative sizes of the subsequent first and second larval generations and the damage they cause. In Canterbury, at least in the absence of parasitism, first generation peaks were generally higher than the second (Goldson *et al*., 1998a), whereas in the Waikato the reverse was true with the second larval generation being the most damaging (Barker & Pottinger, 1982).

Parasitoid effects

Although peripheral to the primary aim of this contribution, results suggest building impacts of parasitism on *L. bonariensis* population dynamics. This is consistent with the observation of Goldson *et al*. (1998a), who found that the impact of parasitism considerably reduced the size of the first summer generation egg and larval peaks. The identification of the ecological factors determining *M. hyperodae* impacts on *L. bonariensis* would be informative for biological control theory and warrants further investigation.

Conclusion

This relatively long-term study has confirmed how important regional and plant cultivar differences can be in influencing the population dynamics of *L. bonariensis*. Canterbury pastures showed none of the resource-regulation of *L. bonariensis* populations identified in the Waikato.

A significant observation in this study is the inverse relationship between *L. bonariensis* adult populations and unrealised fecundity, possibly indicating a pheromonal spacing effect. This presents opportunity to advance theoretical insight into the interactions between parasitism and the mechanisms that lead to unrealised fecundity.

Acknowledgements

The authors thank their colleagues John Proffitt and Mark McNeill who collected and collated much of the data and freely shared their expertise. Thanks also to Dr Brian Manly of West Inc. for his advice on life table analysis.

The authors acknowledge the funding for this research via the New Zealand Foundation for Research, Science and Technology.

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