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The Demographic Performance of the Capitulum Weevil, *Larinus latus*, on Onopordum Thistles in its Native and Introduced Ranges

W. J. PETTIT and D. T. BRIESE

CRC for Weed Management Systems and CSIRO Entomology,
GPO Box 1700, Canberra 2601, Australia

Abstract

It is a widely held premise amongst biological control practitioners that an agent released into a new range free from constraints such as specific natural enemies will perform better than in its native range. However, differences in performance between an agent in its introduced and native range have seldom been quantified to test this premise. The release of the capitulum weevil, *Larinus latus*, for the control of *Onopordum* spp. thistles in Australia has provided an opportunity to do so. In 1996/97, four years after establishment of the weevil, data were collected on population density, capitulum attack rates, oviposition rates, developmental success and patterns of oviposition. Data from this population, which is still expanding and not yet resource limited, were compared and contrasted with data from a similar study of this agent in its native range in Greece, where populations of *L. latus* were found to be relatively stable and were influenced by predation and competition. The data confirmed greater survival in the absence of predators, but also indicated that basic demographic parameters such as fecundity can also change when an agent is displaced into a new environment.

Keywords: Biological control, *Larinus latus*, *Onopordum*, comparative demography

Introduction

It is a common premise that biological control agents will perform better in the area of introduction than in their native range. Freedom from the constraints of specialised natural enemies that limit population growth of the agents in their native range is the most widely invoked reason for this (see Sheppard and Woodburn 1996). However, this has rarely been tested and, when done, other demographic factors, such as intraspecific competition and host-agent asynchrony seem to nullify any advantage due to reduced mortality from natural enemies (Sheppard and Woodburn 1996). Clearly, any differences between the demographic performance of an introduced agent in its new and native ranges are important, both for initial establishment and later impact on the target weed.

The capitulum weevil, *Larinus latus* Herbst, was studied in its native range in Greece to evaluate its potential for the control of *Onopordum* thistles in Australia. Detailed data were collected on different demographic parameters, such as fecundity, oviposition pattern and survival of different life-stages, of a field population of *L. latus* in Greece (Briese 1996a,b). Following release in Australia in 1992, the weevil has established and populations have gradually increased and dispersed from the release sites (Woodburn and Briese 1996). This paper describes the demographic performance of *L. latus* at one of the initial release sites in Australia, and then compares and contrasts this with measurements obtained for the weevil in its Greek native range. Finally, it considers how this might affect the potential of *L. latus* to control *Onopordum* thistles.

Material and Methods

The study populations

Larinus latus is a large weevil (12-20mm long) and is one of the most common insects found on *Onopordum* thistles in Greece (Briese *et al.* 1994). *L. latus* adults become active in spring at the time of stem elongation in their host plants. They feed on leaf tissue and, once capitulum development commences the females bore a hole into the upper stem or capitulum and lay a single egg, which they cover with a faecal cap. Upon hatching, the larvae bore into the capitulum where they feed on receptacle tissue and developing seeds. The development of *L. latus* from egg to emerging adult takes approximately six weeks. Adults emerge from dehiscing capitula in late summer, are inactive through autumn and winter, and commence mating in mid-spring. The population of *L. latus* studied in Australia had been established for a period of 4 years and occurred on an infestation of *O. acanthium* L. at Lanyon (35°29'S x 149°05'E), 25km south of Canberra. *O. acanthium*, *O. illyricum* and their hybrids are the primary targets of biological control in Australia. A description of the site is given in Pettit *et al.* (1996). A description of Epanomi, the site at which the original demography data were collected *for L. latus* in Greece, is given in Briese (1996a). This population occurred on *O. bracteatum*, the most common species of *Onopordum* in Greece, but the weevil does attack both target species of *Onopordum* (Briese *et al.* 1994). Some differences between *O. acanthium* and *O. bracteatum*, and between the infestations used in this study, that could affect oviposition behaviour and survival of *L. latus* are listed in Table 1. In particular, *O. acanthium* has generally smaller capitula, with narrower involucral bracts. Both species flower at a similar time, *but O. acanthium* flowers for a longer period.

Table 1.
Differences between *Onopordum* infestations at Lanyon, Australia, and Epanomi, Greece.

	Lanyon	Epanomi
Onopordum species	*O. acanthium*	*O. bracteatum*
Capitulum size range (mm)	18-44	15-63
Capitula / plant (mean plus range)	28 (6-59)	9 (3-24)
Flowering period (days from winter solstice)	46 (169-218)	37 (179-216)
Plant density per m^2 (95% C.L.)	3.5 (2.3-7.3)	0.7 (0.6-0.9)

Sampling procedures

The demographic performance of *L. latus* at the Lanyon site was measured similarly to that described by Briese (1996a) for the Greek population.

Oviposition

Twenty plants were selected at random within the study area. Plant height and the locations of all capitula on each plant were recorded. At intervals of three to four days the number and position of *L. latus* eggs on each capitulum were recorded. At the same time, the size of each capitulum was measured and flowering phenology recorded as green bud, in flower or mature.

Fecundity

When eggs were first noticed in the field, fifteen male-female pairs of *L.latus* adults were collected from *Onopordum* plants in the vicinity of the study site. Each pair was placed into a small mesh fabric bag and placed over one to three *Onopordum* capitula at the study plot. Every three to four days the bag containing the mating pair was moved to fresh capitula until the female died or ceased ovipositing. At each transfer of a mating pair the number of eggs laid on the capitula was recorded and the capitula bagged to protect them from being overlaid by wild *L. latus* in the study area.

Survival of immature stages

At the end of the flowering period all capitula from the marked plants and from the plants that had been exposed to the captured mating pairs were collected, placed individually in paper bags, and brought back to the CSIRO Entomology laboratory. They were then dissected and the presence of larvae, pupae, unemerged adults and empty development cells was recorded for each capitulum.

Results

***Larinus* demography in its introduced range**

As had been observed in the native range in Greece, *L. latus* oviposition was tightly linked to host plant phenology at the Australian site (Fig. 1). Females commenced laying on capitula as soon as they attained a suitable size and continued until virtually all capitula had finished flowering. There was an initial burst of egg laying followed by a decline, possibly due to movement of female weevils away from the monitored plants. However, once flowering commenced, oviposition followed the flowering pattern of capitula quite closely (Fig. 1). As was observed in Greece (Briese 1996b), there was a strong preference for flowering capitula at all sampling periods (X^2_{15}= 227.0, $P<0.001$) in which they were available and, in total, 94.6% of eggs were laid on flowering capitula after 20/12/96.

Comparison of oviposition patterns and fecundity

Female *L. latus* lived longer on *O. acanthium* in Australia than they did on *O. bracteatum* in Greece (Fig. 2). They also laid more eggs per day over the oviposition period (Fig. 2). This is related in part to the longer period when capitula are available for oviposition. Adult weevils feed on leaves and flowers, and, as eggs are continually developing in the ovaries of females, food availability and quality can affect fecundity. In south-eastern Australia, summer rainfall may keep the host-plant in better condition as a food source for weevils than in Greece, where plants senesce more rapidly under the dry Mediterranean-

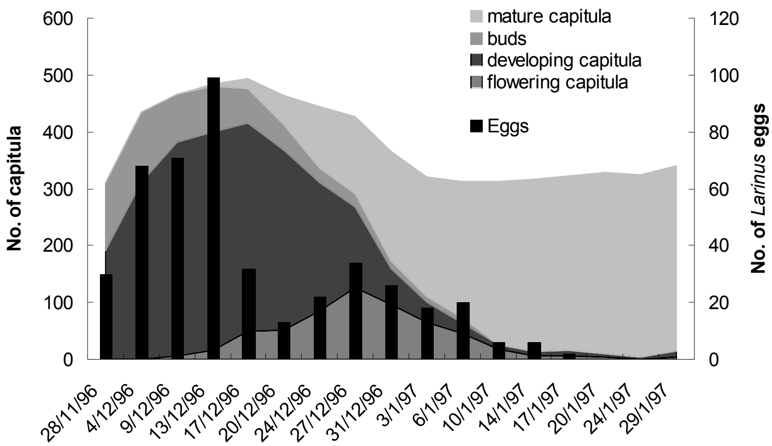

Fig. 1. Oviposition pattern of *Larinus latus* relative to resource availability at Lanyon, Australia (developing capitula were larger than 10mm in diameter).

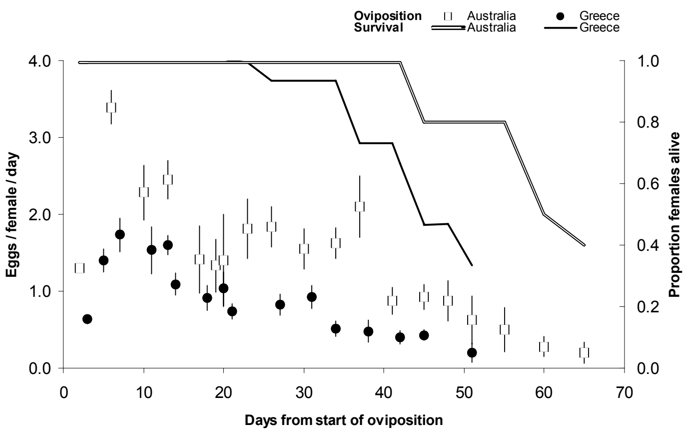

Fig. 2. Comparison of the age-specific fecundity and mortality of *Larinus latus* females at Lanyon, Australia, and Epanomi, Greece.

type summer. This may also contribute to the greater overall fecundity of the weevil in Australia.

Comparison of survival patterns

L. latus fecundity in Australia was almost double that recorded for Greece (Table 2). Moreover, there were no losses to parasitism in the egg or larval stages, nor to competition from other capitulum insects, in the introduced range (Table 2). In contrast, losses at the egg stage were much higher on *O. acanthium* in Australia than on *O. bracteatum* in Greece (Table 2). Some losses at this stage are due to desiccation of eggs when the developing capitula expand and they become exposed. It seems that the finer bracts of *O. acanthium* increase the risks of this mortality factor, as an egg can be lodged against several narrow bracts, which subsequently expand and expose the egg to desiccation or make it

Table 2.
Comparison of fecundity and stage-specific mortality for *Larinus latus* on capitula exposed to, or protected from, natural enemies at Lanyon, Australia, and Epanomi, Greece.

	Australia		Greece	
Exposure to predation/parasitism	Natural	Protected	Natural	Protected
		n=4 *		n=10
Fecundity (mean and range)		63.5 (49-74)		35.4 (18-47)
Egg to larval establishment	n=126	n=417	n=475	n=235
Eggs / attacked capitulum (mean and range)	1.6 (1-5)	2.3 (1-9)	2.8 (1-6)	2.9 (1-10)
Egg parasitism	0	0	20.1%	0
Other pre-establishment losses	62.7%	65.2%	37.1%	38.8%
Larva to adult	n=47	n=145	n=203	n=144
Larvae / entered capitulum (mean and range)	1.2 (1-3)	2.0 (1-6)	1.4 (1-4)	2.3 (1-6)
Larval parasitism	0	0	14.8%	0
Interspecific competition	0	0	18.6%	0
Other post-establishment losses	8.5%	9.2%	12.8%	25.6%
Egg to adult emergence	31.7%	31.9%	23.4%	45.5%
Potential for increase (F1 females per female)	11.3	11.4	4.2	7.7

* The reduced data set for fecundity in Australia was due to grazing of some bagged capitula by cattle in the study area. Calculations of fecundity based on eggs/day and lifespan indicate an average fecundity of 72 eggs/day (n=10) confirming a higher fecundity in Australia.

more difficult for hatching larvae to penetrate the capitulum. Once established though, most larvae survived. Overall, survival to adulthood in the introduced range on *O. acanthium* was higher than on *O. bracteatum* in the native range under natural conditions, but less than that experienced when the weevil was protected from natural enemies (Table 2). Coupled with a higher fecundity in the introduced range, this has enabled *L. latus* to increase slowly in numbers and disperse from the initial release sites.

These data were obtained in an enclosure to prevent interference from stock. However, data collected from outside the enclosure indicated an additional mortality factor due to grazing of the capitula by cattle. This was not a normal occurrence, but during the 1997/98 season 70-80% of capitula were eaten. Cattle in this paddock had previously been observed to eat only the occasional capitulum in non-drought periods. In fact, a herd in a neighbouring paddock into which *L. latus* had dispersed, but was at a much lower density than at the study site, only removed a small proportion of *Onopordum* capitula during the study period. The reason for this is not certain, but Harris (1990) and Story *et al.* (1995) have reported selective grazing by deer, mice and birds on *Centaurea* capitula containing overwintering *Urophora* seed fly in North America. It is possible that the presence of substantial numbers of *L. latus* larvae in capitula may have proved attractive to the cattle and "conditioned" the animals to graze them. While such behaviour is detrimental to *L. latus* populations, it adds value to their impact by increasing the overall level of seed destruction. With the provision of refuges from which the weevils could continually invade stocked paddocks, it is tempting to speculate that a comparatively small population of weevils could have a substantially larger impact through such an interaction. This warrants further examination.

Discussion

The life-cycle of *L. latus* is strongly linked with that of its host plants in both countries of origin and introduction, and similar patterns in oviposition behaviour were observed. In both areas, adult mortality remained low until plants started to senesce and oviposition sites were no longer available, despite this being a longer time period in Australia. Such phenotypic plasticity augurs well for successful biological control, as it ensures that all capitula produced may be targets for attack. This is in contrast with some biological control agents, such as the seed weevil, *Rhinocyllus conicus* on the thistle, *Carduus nutans*. This species has a more rigid life-cycle and, in Australia, oviposition ceases well before flowering of the host plant has terminated, providing a substantial period of escape from seed predation for the target weed (Woodburn and Cullen 1993).

These studies indicate that there has been an escape from natural enemies following release of *L. latus* in the country of introduction. However, reduced larval mortality due to predation and parasitism has been mediated by poorer survival between oviposition and the establishment of larvae within capitula. Much of this seems due to physical stress mediated by the different capitulum phenologies of *O. acanthium*, the host-plant in Australia, and *O. bracteatum*, the host-plant in Greece. Furthermore, differences in rainfall patterns between countries of origin and introduction can also affect fecundity, through their effect on plant growth and condition.

Clearly, escape from natural enemies is not the only factor influencing the demography of a biological control agent in its introduced range. Differences may occur in other mortality factors and fecundity may also differ. Host-plant characteristics (particularly if different species are involved in the native and introduced ranges), the effect of climatic and/or environmental differences on the host-plant and the presence of grazing animals, in a pasture situation, may be important in determining the extent to which this happens. These possibilities should be taken into account, to optimise the chances of agent establishment in the first instant and to maximise their subsequent impact.

Acknowledgments

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References

Briese, D.T. 1996a. Life history of the *Onopordum* capitulum weevil *Larinus latus* (Coleoptera: Curculionidae). Oecologia 105: 454-463.

Briese, D.T. 1996b. Oviposition choice by the *Onopordum* capitulum weevil *Larinus latus* (Coleoptera: Curculionidae) and its effect on the survival of immature stages. Oecologia 105: 464-474.

Briese, D.T., A.W. Sheppard, H. Zwölfer, and P.E. Boldt. 1994. Structure of the phytophagous insect fauna of *Onopordum* thistles in the northern Mediterranean basin. Biol. J. Linn. Soc. 53: 231-253.

Harris, P. 1990. Environmental impact of introduced biological control agents, pp. 289-300. *In* Harris, P. *et al.* [eds.], Critical Issues in Biological Control, Intercept, Andover.

Pettit, W.J., D.T. Briese, and A. Walker. 1996. Aspects of thistle population dynamics with reference to *Onopordum.* Plant Prot. Quart. 11: 232-235.

Sheppard, A.W., and T.L. Woodburn. 1996. Population regulation in insects used to control thistles: Can this predict effectiveness? pp. 277-290. *In* Frontiers of Population Ecology, Floyd, R.B., A.W. Sheppard, and P.J. De Barro [eds.], CSIRO, Melbourne.

Story, J.M., K.W. Boggs, W.R. Good, L.J. White, and R.M. Nowierski. 1995. Cause and extent of predation on *Urophora* spp. larvae (Diptera: Tephritidae) in spotted knapweed capitula. Environ. Entomol. 24: 1467-1472.

Woodburn, T.L., and D.T. Briese. 1996. The contribution of biological control to the management of thistles. Plant Prot. Quart. 11: 250-253.

Woodburn, T.L., and J.M. Cullen. 1993. Effectiveness of *Rhinocyllus conicus*, a biological control agent for *Carduus nutans* in Australia, pp. 99-103. Proceedings, 10th Australian and 14th Asian-Pacific Weeds Conference, September 1993, Brisbane, Australia.