Oviposition behaviour of biological control agents for Paterson's curse (Echium plantagineum L. Boraginaceae)

Jodie Hawley1,2, Helen Spafford Jacob1,2, Paul Wilson1 and Geoff Strickland1,3

1CRC for Australian Weed Management
2School of Animal Biology, University of Western Australia, Crawley, Western Australia 6009, Australia
3Department of Agriculture Western Australia, South Perth, Western Australia 6151, Australia

Summary This study investigates the preferences for oviposition site of two biological control agents for Paterson's curse (Echium plantagineum L. Boraginaceae): Mogulones geographicus (Goeze) (Coleoptera: Curculionidae) and Longitarsus echii (Koch) (Coleoptera: Chrysomelidae). We sought to determine if the presence of a third agent, Mogulones larvatus (Goeze) (Coleoptera: Curculionidae), would deter adult females of the other species from laying eggs on Paterson’s curse rosettes. Adult females of M. geographicus and L. echii were given a choice for oviposition between plants that had been previously attacked by M. larvatus or undamaged plants. L. echii demonstrated no preference for either undamaged plants or those that had been attacked by M. larvatus but M. geographicus chose to lay its eggs on undamaged plants. The results of these experiments suggest that M. geographicus and M. larvatus are unlikely to compete directly in the field because females of M. geographicus avoid laying their eggs on those plants already harbouring M. larvatus. However, L. echii larvae are more likely to be in direct competition with M. larvatus larvae because L. echii adult females do not appear to distinguish between the plants with and without M. larvatus.

Keywords Biological control, oviposition preference, indirect competition.

INTRODUCTION
Echium plantagineum L. (Boraginaceae), commonly known as Paterson’s curse, is an important pasture weed originating from south-western Europe. It now infests 33 million hectares across southern Australia (Swirepik and Smyth 2002) resulting in estimated losses of up to $250 million per annum (Piggin and Sheppard 1995). Several biological control agents against E. plantagineum have been released in Australia. Of these Longitarsus echii (Koch) (Coleoptera: Chrysomelidae), Mogulones geographicus (Goeze) and M. larvatus (Goeze) (Coleoptera: Curculionidae) are the most damaging (Wapshere 1985). The larvae of these three insects feed on different parts of the weed’s roots. Longitarsus echii feeds on the secondary roots, Mogulones geographicus feeds on the taproot and M. larvatus feeds on the crown. M. geographicus emerges one month after M. larvatus, and L. echii emerges even later (Wapshere 1982, Vayssieres and Wapshere 1983). The spatial separation of the larvae and the temporal separation of the adult emergence is thought to alleviate direct competition between M. larvatus and M. geographicus (Forrester 1993). However, there has been no investigation into the possibility of indirect interactions between these two insects or that of L. echii mediated by E. plantagineum.

Indirect interactions occur when one species affects a second species through a change in a third species. For example, a plant can mediate the interactions between two insect herbivores that both rely solely on that plant. This type of interaction can change the population distribution, behaviour, morphology or physiology of the species involved. A decrease in oviposition on leaves damaged by competitors has been found in insects (Faeth 1986, Fowler and MacGargin 1986, McDonald and Sears 1992, Sadras et al. 1998, Cronin and Abrahamson 2001) and this avoidance behaviour may be a mechanism by which insect herbivores reduce competition.

We sought to evaluate whether the oviposition behaviour of M. geographicus and L. echii would be influenced by the presence of M. larvatus in the host plant, E. plantagineum.

MATERIALS AND METHODS
E. plantagineum seedlings were collected from the Department of Agriculture, Entomology Section, South Perth, Western Australia in June 2002 and transplanted into pots of white sand in a glasshouse. After one month, 60 seedlings of 10 cm in diameter were transplanted in pairs into 30 rectangular plastic boxes (32 cm × 42 cm × 13 cm) with drainage holes drilled in the bottom, one plant at each end, and left to grow for another month until they reached 20 cm in diameter.

Two litre bottle cages were put on top of each plant in the boxes and a male and female pair of M. larvatus adults were added randomly to one of the two plants in each box. The cages were left for one week to allow M. larvatus to lay eggs on the plant. The bottle cages
and *M. larvatus* adults were then removed from the plants and the plants were left for one week to allow the larvae to hatch and start feeding. Twenty boxes were chosen making sure that the plants that were attacked and the plants that were not attacked were at a similar stage in their growth and development (determined by visual inspection). This meant they were a similar size and both plants were starting to produce stems. One male and one female *M. geographicus* were added to each of ten of these boxes; one male and one female *L. echii* were added to the ten boxes remaining. Virus mesh was then used to cage the insects in the boxes which were placed on greenhouse benches along an east-west axis. The plants infested with *M. larvatus* were randomly assigned to the east or west position. The insects were left to oviposit on the plants for one week and then removed. The plants were then dissected under a dissecting microscope. *M. geographicus* eggs were found in the blade and petiole of the leaves and *L. echii* eggs were found near the root collar. For *L. echii* the soil immediately around the root collar was also searched for eggs. The number of eggs per plant was recorded.

Replicates where insects died or did not lay any eggs were not included in the analyses. To test the effect of the treatments on oviposition preference, a generalised linear regression model was fitted with a Poisson distribution and a logarithmic link. The presence of *L. echii* in a plant influenced the number of eggs subsequently laid by the two species was evaluated. An interaction between the species of insect and the damage to the plant was also evaluated.

**RESULTS**

Most of the insects offered a choice between plants attacked by *M. larvatus* and undamaged plants laid eggs (*L. echii* = 7; *M. geographicus* = 8). The response of the two insect species to attacked and undamaged plants was significantly different ($X^2 = 17.8$, df = 3, $P < 0.001$). Further investigation into the individual species’ preference found that *M. geographicus* females laid 1.7 times more eggs on undamaged plants than attacked plants ($X^2 = 6.01$, df = 1, $P = 0.014$). *L. echii* laid 1.8 times, but not significantly more eggs on plants that were attacked by *M. larvatus* than undamaged plants (Figure 1; $X^2 = 3.64$, df = 1, $P = 0.056$).

A parasitoid was found in eleven *M. geographicus* eggs in three replicates. Ten of these eggs were laid on plants that were previously attacked by *M. larvatus* and only one was found on an undamaged plant. Of the three treatments that had been attacked by the parasitoid, 48% of the eggs laid on the attacked plants were parasitised while only 6% of the eggs laid on the undamaged plants were parasitised. No parasitoids were noted in *L. echii* eggs.

**DISCUSSION**

The presence of *M. larvatus* in a plant influenced the oviposition behaviour of *M. geographicus* but not *L. echii*. The results from the experiment supported the hypothesis that *M. geographicus* would choose plants that had not been previously attacked by *M. larvatus*. This preference suggests that *M. geographicus* females can distinguish between host plants where a competitor might already be present and thus avoid situations where the survival of their offspring might be jeopardised.

*L. echii* did not have a preference for either attacked or undamaged plants but laid more eggs on plants attacked by *M. larvatus*. This suggests that the larvae of *L. echii* are more likely to be in direct competition with *M. larvatus* than *M. geographicus*.

The difference in response between the two species could be a consequence of evolutionary history. The congeneric and host-specific *Mogulones* species may have adapted to sharing a resource through spatial resource partitioning, temporal differences in adult emergence and oviposition activity, and through oviposition avoidance strategies by *M. geographicus* mediated by cues produced by *E. plantagineum*. Consequently, *M. geographicus* and *M. larvatus* will probably be found on different plants and not compete directly in the field.

On the other hand, *L. echii* did not display avoidance behaviour to plants attacked by *M. larvatus*. Although these beetles have temporal and spatial

![Figure 1. Total number of eggs laid over all replicates after Longitarsus echii (Le) and Mogulones geographicus (Mg) were given a choice to oviposit on either plants that had been previously attacked with M. larvatus or undamaged plants.](image-url)
separation on the plant, they do not appear to be deterred by the presence of *M. larvatus*. Consequently, *L. echii* will probably compete directly in the field with *M. larvatus* and possibly with *M. geographicus*. If such competition is found to reduce the survival and overall impact of either *L. echii* or *M. larvatus*, then the presence of both agents in the same place could reduce the overall effectiveness of the biological control. Field studies and further laboratory studies could clarify this concern and contribute to release recommendations.

The unexpected finding of egg parasitism suggests there may be other biological factors mediating the interaction between the two *Mogulones* species. Unfortunately the parasitoid was unable to be identified. However, further studies to investigate the parasitoid’s response to different phenolics and plant chemicals and its ability to find a host would be valuable. If the parasitoid is able to locate *M. geographicus* eggs more readily in the field when they are laid on plants with *M. larvatus*, then the survival rate of *M. geographicus* would also decrease on these plants. This is the first reported case of parasitism of either *Mogulones* species by a parasitoid in Australia.

**ACKNOWLEDGMENTS**

Thanks to the CRC for Australian Weed Management for funding this project and to Alan Lord, Department of Agriculture Western Australia, for his help. Thanks are also given to Matthew Smyth for helpful comments.

**REFERENCES**


