

The Biological Control Agent *Acanthoscelides macrophthalmus* (Chrysomelidae: Bruchinae) Inflicts Moderate Levels of Seed Damage on Its Target, the Invasive Tree *Leucaena leucocephala* (Fabaceae), in the KwaZulu-Natal Coastal Region of South Africa

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The biological control agent *Acanthoscelides macrophthalmus* (Chrysomelidae: Bruchinae) inflicts moderate levels of seed damage on its target, the invasive tree *Leucaena leucocephala* (Fabaceae), in the KwaZulu-Natal coastal region of South Africa

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Leucaena leucocephala (Lam.) de Wit (Fabaceae), an agroforestry tree with invasive properties, was targeted for biological control in South Africa. The seed beetle *Acanthoscelides macrophthalmus* (Schaeffer) (Chrysomelidae: Bruchinae) was released in 1999 to curb its excessive seed production without negating its beneficial properties. The adult beetles oviposit on the seed pods and loose seeds of *L. leucocephala* and the hatching larvae enter the seeds and destroy them during their development. Although the beetle has become widely established in South Africa, its contribution to the weed's management is unknown. The aims of this pilot study were to assess: (i) the levels of seed damage inflicted by *A. macrophthalmus* on *L. leucocephala* populations and; (ii) the extent to which the endophagous immature stages have recruited native parasitoids. The study was carried out over seven months at three sites in the KwaZulu-Natal coastal region, where *L. leucocephala* is abundant. Mean seed damage was inconsistent, with considerable variation (2–62 %) between sites and time of collection. On average, <30 % of available seeds was damaged at each site. Five species of parasitoids (Hymenoptera: Chalcidoidea) were consistently reared from beetle-damaged seeds, two of which (both Pteromalidae) were most commonly associated with the beetles. Mean mortality resulting from parasitism was similarly inconsistent and variable (1–22 %) between sites and time of collection. Although parasitism increased with increased seed damage, on average only 7–9 % of larvae/pupae were parasitized at the three sites. The modest levels of seed damage recorded in this study appear insufficient to regulate populations of *L. leucocephala* in South Africa.

Key words: agent parasitism, invasive plants, leucaena, seed beetles, weed biocontrol.

INTRODUCTION

Leucaena leucocephala (Lam.) de Wit (leucaena; Fabaceae), a small tree of Central American origin, has become invasive in several tropical and subtropical regions worldwide following deliberate introductions for agroforestry (Hughes 2006). Conditions in South Africa are largely suboptimal, with invasions currently confined to the eastern, subtropical, higher rainfall areas, notably the KwaZulu-Natal coastal region (Henderson 2001; Olckers 2011). However, these plants are able to persist in harsh environments where they fix nitrogen, grow rapidly and produce excessive numbers of seeds (Orwa *et al.* 2009). Despite the plant's many agroforestry benefits (Orwa *et al.* 2009), it invades riparian zones, forest margins and urban wastelands, displacing natural vegetation and facilitating the invasion of other alien plant

species (Henderson 2001; Yoshida & Oka 2004). Given these concerns, biological control using the seed beetle *Acanthoscelides macrophthalmus* (Schaeffer) was initiated in South Africa in 1999, in an attempt to halt the spread of the weed while retaining its beneficial properties (Olckers 2004; Shoba & Olckers 2010; Olckers 2011).

Seed beetles (Chrysomelidae: Bruchinae, previously called Bruchidae) have been deployed against invasive leguminous trees that produce excessive amounts of seed, with generally inadequate levels of success in South Africa (*e.g.* Hoffmann *et al.* 1993; Coetzer & Hoffmann 1997; Impson *et al.* 1999; Byrne *et al.* 2011; Zachariades *et al.* 2011) and elsewhere in the world (*e.g.* Radford *et al.* 2001; Van Klinken 2005; Van Klinken & Flack 2008; Van Klinken *et al.* 2009). Females oviposit on the seed pods or seed surfaces and the hatching larvae burrow into the seeds, consuming

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the contents before pupating and emerging as adults (e.g. Southgate 1978; Miller 1994). Besides becoming widely established in South Africa (Olckers 2011), *A. macrophthalmus* has also inadvertently become established in several other countries, notably Australia (Raghu *et al.* 2005), West Africa (Delobel & Johnson 1998; Effowe *et al.* 2010), the USA (Florida and Hawaii) (Kingsolver 2004) and southeastern Asia (Tuda 2007), presumably *via* introduction in contaminated seeds.

In the absence of any post-release evaluations, an assessment of the levels of seed damage in South Africa was required to determine the likely contribution of *A. macrophthalmus* to the weed's control, particularly since it is widely held that very high levels of seed damage (95–99 %) are required to regulate populations of invasive trees with very high seed loads (e.g. Hoffmann & Moran 1998; Kriticos *et al.* 1999; Van Klinken *et al.* 2008). Bruchine beetles are, however, erratic in their exploitation of seeds (e.g. Coetzer & Hoffmann 1997; Radford *et al.* 2001) and an earlier study on *A. macrophthalmus* (Egli & Olckers 2012) indicated that canopy-held seeds of *L. leucocephala* were more susceptible to exploitation than dehisced seeds on the soil surface.

The endophagous immature stages of *A. macrophthalmus* are vulnerable to parasitism in the field in South Africa (Shoba & Olckers 2010) and elsewhere in the world (Delobel & Johnson 1998; Raghu *et al.* 2005). In particular, several species of parasitic Hymenoptera are associated with the immature stages of native Bruchinae that exploit the seeds of native species of *Acacia s.l.* in South Africa (Impson *et al.* 1999) and these are most likely to have included the introduced *A. macrophthalmus* in their host range. Excessive and density-dependent parasitism of the immature stages inside the seeds will result in substantially fewer adults emerging, thus decreasing population densities.

The canopies of *L. leucocephala* populations typically contain seeds all year round in several countries of introduction (Orwa *et al.* 2009), albeit at varying densities determined by plant phenology (*i.e.* cycles of pod set and dehiscence). However, both seed damage by *A. macrophthalmus* and parasitism of its immature stages may be inconsistent and seasonal. It is thus possible that at certain times of the year *A. macrophthalmus* will be less effective at exploiting the seeds of *L. leucocephala*, whether or not related to parasitism.

This study follows up on questions raised in a recent review of the project on *L. leucocephala* (Olckers 2011) and was initiated to obtain a rapid assessment of the potential impact of *A. macrophthalmus* in South Africa over a seven-month period, particularly: (i) the levels of damage in canopy-held seeds, which are preferred for oviposition and; (ii) the extent to which the endophagous immature stages have become parasitized.

MATERIAL AND METHODS

Study sites

These comprised three localities in the KwaZulu-Natal coastal region which is typified by dense populations of *L. leucocephala* that support populations of *A. macrophthalmus*. The three study sites were in relatively close proximity to each other and located at Amanzimtoti (30°01'59"S 30°53'26"E); Durban (29°48'29"S 30°58'54"E) and Verulam (29°40'47"S 31°02'09"E).

Sampling procedure

On each sampling occasion, seeds were collected from the canopies of 10 randomly selected, pod-bearing trees at each site. Ten intact ripe pods were removed from each tree and placed into a Ziploc™ bag, taking care not to dislodge the seeds during collection. The bags were placed in a cool box and returned to the insectary at the University of KwaZulu-Natal, Pietermaritzburg. The seeds from each sample of 10 pods were then removed and placed in 500 ml plastic containers which were maintained at 28 °C to monitor beetle and parasitoid emergence. Sampling was carried out over seven months, from April to October 2010, with a total of 210 trees sampled (70 per site) during this time.

For each tree sampled, beetle and parasitoid emergence was recorded for 35 days, with inspections of the containers every two days. While 35 days represents the average time taken by the beetle to develop from egg to adulthood at 28 °C (Shoba & Olckers 2010), parasitoids were observed to develop considerably more quickly. Emerging beetles were removed at every inspection to prevent them from reaching sexual maturity (three days on average (Shoba & Olckers 2010)) and ovipositing on the seeds, which would have caused over-estimation of seed damage levels. After 35 days, all of the eggs laid prior to

collection were assumed to have produced adults and the inspections were terminated. Emerging parasitoids were also removed at each inspection and identified to family level using a key (Prinsloo 1980).

Data recorded for each sampled tree included the numbers of seeds collected, the numbers that were damaged by *A. macrophthalmus* and the numbers of beetles and parasitoids that emerged from these. Damaged seeds contained emergence holes of adult beetles or parasitoids; those of the beetles were easily distinguishable from those of the parasitoids because of their larger size. Numbers of damaged seeds were easily reconciled with numbers of emerging beetles and wasps, because individual *L. leucocephala* seeds mostly support the development of a single beetle/wasp, with more than one beetle emerging per seed rarely recorded in the field (Raghu *et al.* 2005).

Statistical analysis

All analyses were conducted using SPSS Statistics 19.0. The numbers of seeds per pod, proportions of seeds that were damaged by *A. macrophthalmus* (including those parasitized) and the proportion of beetles that were parasitized were compared between sites and months sampled. Data on seeds per pod met the assumptions of normality and homogeneity of variances and were thus analysed with two-way ANOVA. There was considerable variation in the remaining data sets which, despite different transformations, did not meet the assumptions of normality and/or homogeneity of variances. Independent Samples Kruskal-Wallis tests were thus used to analyse seed damage and parasitism for the overall data set ($n = 210$ trees) and within each of the three sites ($n = 70$ trees). Spearman's rank-order correlation was used to determine the relationship between the number of emerging parasitoids and the number of beetle-damaged seeds in the 210 trees sampled.

RESULTS

Seed damage by *A. macrophthalmus*

During the seven months of the study, a total of 39 035 seeds were collected from the 210 trees that were sampled at the three sites, giving an overall average of 186 seeds sampled per tree and 19 seeds sampled per pod. While numbers of seeds per pod were not influenced by month of the year

($F = 1.871$, d.f. = 6, $P = 0.088$), they were influenced by site ($F = 19.804$, d.f. = 2, $P < 0.0005$) and the interaction between month and site was also significant ($F = 2.231$, d.f. = 12, $P = 0.012$). Mean (\pm S.E.) numbers of seeds per pod were significantly different between all three sites, with higher numbers recorded at Amanzimtoti (19.7 ± 0.3) than at Durban (18.7 ± 0.3) and Verulam (17.4 ± 0.3).

The mean percentages of seeds damaged by *A. macrophthalmus* over the seven-month study period were variable and inconsistent within and between the three sites (Fig. 1). Percentage seed damage varied significantly ($H = 127.184$, d.f. = 20, $P < 0.0005$) between the 21 sampling events (3 sites \times 7 months) and between months at each of the Amanzimtoti ($H = 44.064$, d.f. = 6, $P < 0.0005$), Durban ($H = 30.568$, d.f. = 6, $P < 0.0005$) and Verulam ($H = 48.209$, d.f. = 6, $P < 0.0005$) sites.

The patterns of seed damage were different at the three sites (Fig. 1). Monthly seed damage at Amanzimtoti varied from 2 % (April) to 46 % (September), compared with 10 % (April) to 49 % (June) at Durban and 2 % (August) to 62 % (June) at Verulam. The monthly trends at Durban and Verulam were similar with initially lower levels of seed damage that increased to peaks in June and then decreased to low levels by September and October. By contrast, seed damage at Amanzimtoti showed a steady increase which peaked in September and October. When seed damage was averaged over the seven months, around 28 % of available seeds were damaged at each of the three sites.

Parasitism of *A. macrophthalmus*

Five species of hymenopteran parasitoids (Chalcidoidea) were consistently reared from beetle-damaged seeds (Table 1), including three species of Pteromalidae which comprised 88 % of the collections and one species each of Eupelmidae (7 %) and Eurytomidae (5 %). Two species of Pteromalidae were most commonly associated with damaged seeds and comprised 56 % and 27 % of the parasitoids reared (Table 1).

The mean percentages of beetle parasitism over the seven-month study period were similarly variable and inconsistent within and between the three sites (Fig. 2). Percentage parasitism varied significantly ($H = 49.381$, d.f. = 20, $P < 0.0005$) between the 21 sampling events (3 sites \times 7 months) and between months at the Amanzimtoti site

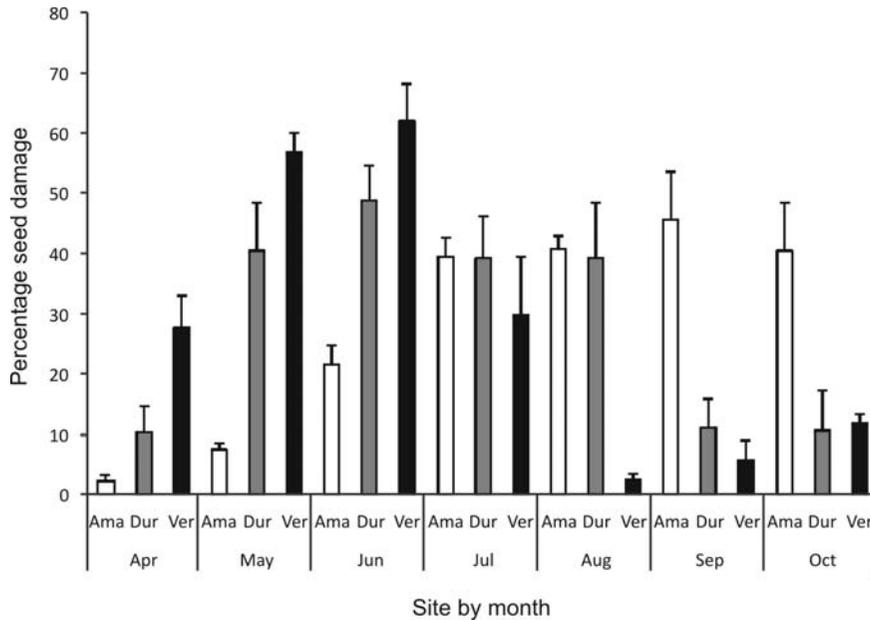


Fig. 1. Mean (\pm S.E.) percentage of *Leucaena leucocephala* seeds from three sites that were damaged by *Acanthoscelides macrophthalmus* over the seven-month survey. White bars = Amanzimtoti (Ama), grey bars = Durban (Dur) and black bars = Verulam (Ver).

($H = 27.726$, d.f. = 6, $P < 0.0005$). However, there were no significant differences in beetle parasitism between months at the Durban ($H = 1.700$, d.f. = 6, $P = 0.945$) and Verulam ($H = 4.782$, d.f. = 6, $P = 0.572$) sites.

Monthly beetle parasitism at Amanzimtoti varied from 1% (May) to 22% (October), compared with 10% (September) to 16% (June) at Durban and 7% (October) to 16% (August) at Verulam. While parasitism at the Durban and Verulam sites were mostly consistent between months, parasitism at Amanzimtoti generally increased over the sampling period. When beetle parasitism was averaged over the seven months,

around 7–9% of available beetle larvae/pupae were parasitized at the three sites.

Despite considerable variation in the levels of parasitism between the 210 trees sampled, there was a significant positive relationship ($y = 0.095x - 0.686$, $r_s = 0.706$, $P < 0.0005$) between parasitoid numbers and numbers of beetle-infested seeds (Fig. 3).

DISCUSSION

Seed damage

Following the trend of other bruchine beetles that were released as biological control agents (e.g. Impson *et al.* 1999; Radford *et al.* 2001; Van Klinken

Table 1. Total numbers of parasitoids reared from seeds of *Leucaena leucocephala* containing immature stages of *Acanthoscelides macrophthalmus* and collected at three study sites over the seven-month survey period.

Parasitoid species (Accession no.)	Apr	May	Jun	Jul	Aug	Sep	Oct	Species total (%)
Pteromalidae sp. 1 (AcTo 1)	7	13	25	16	48	53	35	197 (26.8)
Pteromalidae sp. 2 (AcTo 2)	41	100	99	51	29	53	41	414 (56.3)
Pteromalidae sp. 3 (AcTo 3)	0	1	4	3	5	21	3	37 (5.0)
Eupelmidae sp. (AcTo 4)	0	1	7	6	5	20	12	51 (6.9)
Eurytomidae sp. (AcTo 5)	0	1	0	1	2	21	12	37 (5.0)
Monthly total	48	116	135	77	89	168	103	736
Percentage	(6.5)	(15.8)	(18.3)	(10.5)	(12.1)	(22.8)	(14.0)	

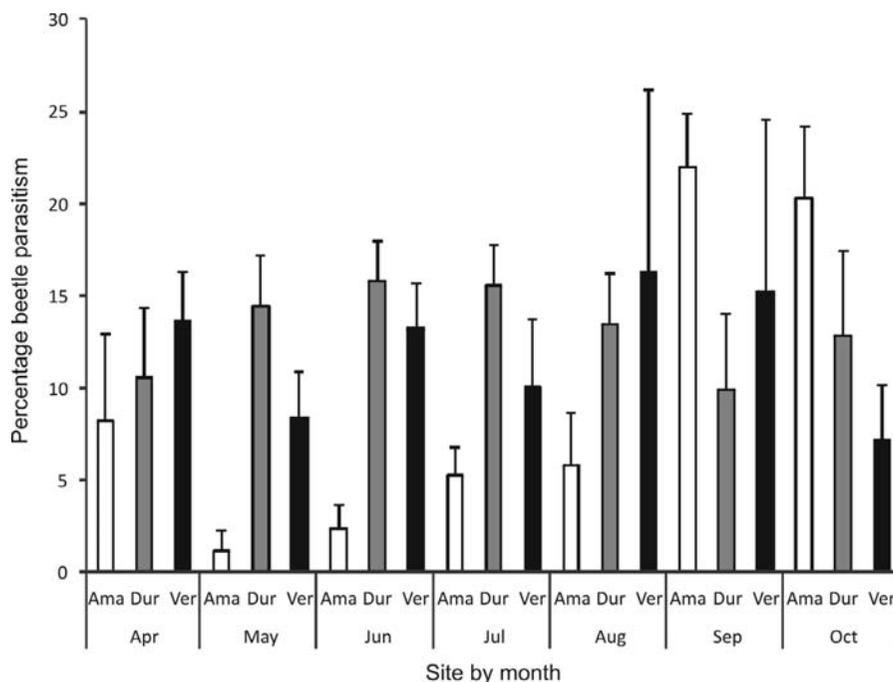


Fig. 2. Mean (\pm S.E.) percentage parasitism of the immature stages of *Acanthoscelides macrophthalmus* inside the seeds of *Leucaena leucocephala* at three sites over the seven-month survey. White bars = Amanzimtoti (Ama), grey bars = Durban (Dur) and black bars = Verulam (Ver).

2005; Van Klinken & Flack 2008; Van Klinken *et al.* 2009), seed damage by *A. macrophthalmus* was somewhat erratic with considerable variation between trees, sites and seasons. Some of this variation may be related to differences in the availability of seed-bearing pods in the canopies for oviposition, as occurred with *A. macrophthalmus* in Australia (Raghu *et al.* 2005). Nevertheless, only moderate levels of seed damage were inflicted by *A. macrophthalmus*, with the highest mean monthly levels seldom exceeding 50 % and overall mean damage levels at each of the three sites falling below 30 %. In order for a seed-feeding agent to regulate populations of its target weed, it needs to destroy 95–99 % of the seeds produced annually (*e.g.* Hoffmann & Moran 1998; Kriticos *et al.* 1999; Van Klinken *et al.* 2008), so as to limit the numbers of viable seeds entering the seed bank and allow other density-dependent factors to reduce seedling recruitment (Andersen 1989). Our data are consistent with the levels of seed damage reported in Australia, which also seldom exceeded 50 % (Raghu *et al.* 2005), and support the contention that *A. macrophthalmus* is incapable of regulating *L. leucocephala* populations on its

own. However, in the case of species like *L. leucocephala*, where the seeds are dehisced and accumulate mostly below or adjacent to the parent plants, the rates of spread, which are more sensitive to seed reductions, may be reduced by such moderate levels of seed damage (Van Klinken *et al.* 2008).

Parasitism

Generally, native parasitoids are less likely to inhibit introduced biological control agents than generalist predators (*e.g.* Cornell & Hawkins 1993; Hill & Hulley 1995). However, five wasp species were consistently reared from seeds infested with *A. macrophthalmus*, three more than recorded in an earlier study (Shoba & Olckers 2010). These were presumed to be parasitizing the larvae or pupae of *A. macrophthalmus*, although Eurytomidae are also known to be hyperparasitoids (Prinsloo 1980). Three of the five parasitoid species were Pteromalidae, which are commonly associated with the endophagous immature stages of bruchine beetles (*e.g.* Prinsloo 1980; Hoffmann *et al.* 1993; Kingsolver 2004; Byrne *et al.* 2011).

Indeed, *A. macrophthalmus* has been proposed

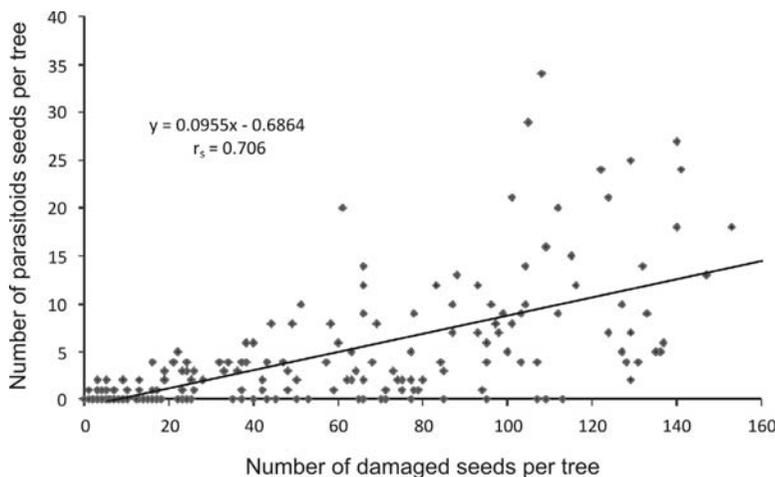


Fig. 3. Relationship between the number of emerging parasitoids and the number of *Leucaena leucocephala* seeds damaged (*i.e.* containing immature stages of *Acanthoscelides macrophthalmus*). Each data point is representative of a sample of 10 pods collected from each of 210 trees sampled at three sites over seven months.

as a surrogate host for the mass-rearing of a pteromalid wasp used for augmentative releases against three bruchine species that are pests of cowpeas in fields and storage containers in Togo (Effowe *et al.* 2010). Eupelmidae and Eurytomidae have also been associated with bruchine beetles (*e.g.* Prinsloo 1980; Kingsolver 2004). There was a moderately strong and density-dependent relationship between parasitoid numbers and numbers of damaged seeds recorded per tree sampled over the seven-month period, suggesting that native parasitoids are targeting the immature stages of *A. macrophthalmus*, and that the association is not sporadic and caused by occasional 'spillover' from native *Acacia* or other legume species.

Although parasitism of the endophagous immature stages of *A. macrophthalmus* was relatively low (7–9 % overall at the three sites), it was considerably higher than that reported for this species (around 1 %) in Australia (Raghu *et al.* 2005). Parasitism of *A. macrophthalmus* was also somewhat higher than that reported in similar studies on bruchines that were released for the biological control of *Prosopis* species (Fabaceae) in South Africa. Despite the recovery of some 24 species of parasitoids from *Prosopis* pods, larval/pupal parasitism of *Algarobius prosopis* (LeConte) and *Neltumius arizonensis* Schaeffer has consistently proven to be <4 % and therefore insufficient to disrupt the beetles' population densities (Hoffmann *et al.* 1993; Coetzer & Hoffmann 1997; Impson *et al.* 1999; Zachariades *et al.* 2011). Given indications of

density dependence, the monthly levels of parasitism reported here (1–22 %) may have a negative influence on population densities and hence levels of seed damage inflicted by *A. macrophthalmus*.

However, the moderate levels of seed damage recorded in this study may be influenced more by other mortality factors, notably in relation to the egg stage. An initial assessment of egg mortality in *A. macrophthalmus* (Egli & Olckers 2012) suggested that only 34 % of eggs produced larvae that successfully penetrated the seeds and that this was caused largely by ant predation. Byrne *et al.* (2011) recorded even higher levels of ant predation of the eggs of *Sulcobruchus subsuturalis* (Pic.), an unsuccessful agent of *Caesalpinia decapetala* (Roth) Alston (Fabaceae) in South Africa. In addition, Coetzer & Hoffmann (1997) recorded up to 80 % parasitism of the eggs of *N. arizonensis* during some months of the year, while Byrne *et al.* (2011) recorded 90 % parasitism of the eggs of *S. subsuturalis* that survived predation. Although initial assessments of egg parasitism were low (Egli & Olckers 2012), egg parasitoids may be similarly disruptive in *A. macrophthalmus* which, like the aforementioned bruchines, also lays its eggs exposed on the seed pods.

CONCLUSIONS

Patterns of seed damage by *A. macrophthalmus* were highly variable in relation to time of year and study site and may be related to seed availability.

The relationship between seed damage and seed availability in Australia was inversely density-dependent (Raghu *et al.* 2005), with levels of seed damage by *A. macrophthalmus* increasing with decreased seed crops because of seed scarcity. To explain the patterns observed in this pilot study, seed damage levels are currently being monitored at additional sites, in relation to the phenology of *L. leucocephala* populations (*i.e.* periods of flowering and pod production). Mortality factors affecting the egg stage are also under evaluation to determine the extent to which these are contributing to the moderate levels of seed damage reported here.

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