Constraints on *Neltumius arizonensis* (Coleoptera: Bruchidae) as a biocontrol agent of *prosopis* in South Africa: the role of parasitoids.

Honours thesis

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Contents

Acknowledgements

Abstract

1. Two species of seed feeding bruchid, *Algarobius prosopis* and *A. bottimeri*, were introduced to South Africa in 1987 and 1990 respectively, to curb the spread of the invasive weed *Prosopis*. Failure of *A. bottimeri* to establish and reduced effectiveness of *A. prosopis* due to interference by livestock resulted in the release of a third species, *Neltumius arizonensis* in 1992.

2. *Algarobius prosopis* populations have remained high but *N. arizonensis* has not been as successful.

3. Populations of both bruchids showed similar emergence patterns through the sampling period hence there is no temporal partitioning of resources.

4. Percentage emergence of *N. arizonensis* was low at the start of the season but increased as the season progressed with higher proportions of *N. arizonensis* emerging from 'tree' pods than 'ground' pods. Regardless of the spatial partitioning of resources by the two bruchids, *N. arizonensis* emergence numbers are still far lower than those of *A. prosopis* (approximately 1:4 respectively).

5. Oviposition strategies of *N. arizonensis* results in high levels of egg parasitism by *Uscana* sp., Trichogrammatidae, that *A. prosopis* escapes by ovipositing in concealed places avoiding detection by parasitoids.

6. Egg parasitism is extremely high on *N. arizonensis* eggs (67%) and has resulted in failure by *N. arizonensis* to establish large populations and hence its effectiveness as a biocontrol agent is negligible.

Introduction

Several *Prosopis* species (Fabaceae) were introduced to southern Africa from North

and South America at the end of the nineteenth century for shade, fuel and fodder

(Harding, 1978). These species have become naturalised and now cover an estimated

180 400 ha in the northwestern and northern Cape (Harding, 1988). The total area

suitable for invasion by *Prosopis* species is estimated at 935 000 ha in the

northwestern Cape alone (Zimmerman, 1991). All *Prosopis* species are currently

listed as invader plants in South Africa.

When it was first proposed that biocontrol methods should be introduced to curb the

spread of the plant there was widespread concern from the farmers who benefitted

from these plants. The pods that are highly nutritious are used for supplementary

feeding for livestock, the wood is used in industry for smoking processed meats and

for firewood and a large apiculture industry has emerged because of the flowers.

Because of this it was decided that only seed feeding insects should be used for

biocontrol of the weed as they do not reduce the nutritional value of the pods (Moran,

1991; Moran *et al*, 1993). Initially two bruchid species, *Algarobius prosopis* (Le

Conte) and *Algarobius bottimeri* (Kingsolver) were introduced. *A. prosopis* was

released in 1987 and *A. bottimeri* in 1990 (Zimmerman, 1991). *Algarobius bottimeri*

failed to establish while the effectiveness of *A. prosopis* had been curbed because the

pods are eaten by livestock and the larvae die before the beetles could utilise and

damage the seeds (Zimmerman, 1991). This resulted in the subsequent release of

another bruchid, *Neltumius arizonensis* Schaeffer (Moran *et al*, 1993) in 1992 that

was supposed to lay eggs on unripe pods in trees (Swier, 1974 as cited in Moran,

1991). If this was so the seeds would be destroyed before the pods fell to the ground

and were eaten by livestock. It was subsequently found that *N. arizonensis* did not utilise immature seeds because the females only lay on mature pods. *A. bottimeri* and *A. prosopis* compete for the same resource and it is thought that this resulted in *A. bottimeri* failing to establish, because of this and in absence of specialist natural enemies (Strathie, 1995 unpublished) expressed concern that *N. arizonensis* and *A. prosopis* would compete too.

The oviposition strategies differ between the two species. *A. prosopis* lays eggs in bunches concealed in cracks in the pods and emergence holes (Zimmerman, 1991), thus lowering the amounts of parasitism (Kistler, 1985). The larvae of *A. prosopis* are highly mobile and are able to crawl through the pod locating seeds without a larva in already (Swier, 1974 as cited in Strathie, 1995 unpublished) and hence reducing competition. *N. arizonensis* reduces competition by carefully inspecting a pod and only laying a single egg above those seeds that have no eggs on them already (Strathie, 1995 unpublished). The larvae are not able to move great distances and are only able to burrow down into the seed directly below the egg (Swier, 1974 as cited in Strathie, 1995 unpublished). *N. arizonensis* larvae are aggressively killed by those of *A. prosopis* if they are competing for the same resource (Hoffmann, *pers. comm.*).

Hoffmann et al (1993) and Coetzer & Hoffmann (1996, unpublished) found that both these species were susceptible to larval and pupal parasitism by a number of indigenous parasitoid species. Larval and pupal parasitism does not occur to any great extent, and it is assumed that both species are equally susceptible to this form of parasitism (Hoffman, *pers. comm.*). Because of *A. prosopis'* method of laying eggs in concealed areas it is not subjected to high levels of egg-parasitism. However, the behaviour of ovipositing an egg on the surface of the pod results in the eggs of *N. arizonensis* having increased susceptibility to egg parasitoids (Coetzer, 1996

unpublished). Coetzer (1996 unpublished) identified one egg parasitoid, *Uscana* sp.,

Trichogrammatidae, responsible for parasitising high levels of *N. arizonensis* eggs,

but in not high enough proportions to affect *N. arizonensis* adversely. Emergence of

N. arizonensis over the 1996 study period was low, twenty times less than that of *A.*

prosopis, and Coetzer concluded that *N. arizonensis* populations were too low to have

a marked effect on *Prosopis*.

The first aim of this study was to determine the proportions of *N. arizonensis* and *A.*

prosopis to verify that there are still differences in the relative abundance of the two

species now that they have been established for several years and the populations

have reached equilibrium levels. The second aim was to determine the levels of

parasitism by indigenous parasitoids on the two bruchid species and investigate

whether this has mediated the relative abundance of the two species.

Methods

This study was undertaken at four sites in the Clanwilliam region namely Onderplaas

farm (31°59' S; 19°15' E, 'O', Fig. 1), Driefontein farm (32°01'S; 19°13' E, 'D', Fig.

1), Clanwilliam (32°10' S; 18°53' E, 'C', Fig. 1) and Piketberg (32°57' S; 18°46' E,

'P', Fig. 1). Pods were collected from the four sites on three occasions, namely

19/03/2000, 24/04/2000, and 30/05/2000. Pods were taken from both the trees and

the ground where possible. 'Tree' pods were those still attached in the canopy and

'ground' pods were those that had fallen to the ground and were lying at the base of

the tree. Clanwilliam and Piketberg had pods in both the trees and on the ground in

adequate numbers for samples to be taken at each of the sampling dates. Driefontein

Farm was a site of active livestock farming and no pods were available on the ground

Fig. 1: Location of the field sites, Clanwilliam (C), Onderplaas (O),
Driefontein (D) and Piketberg (P) in Western Province,
South Africa. CT represents Cape Town, (after Coetzer, 1996)

1 cm represents 50 km
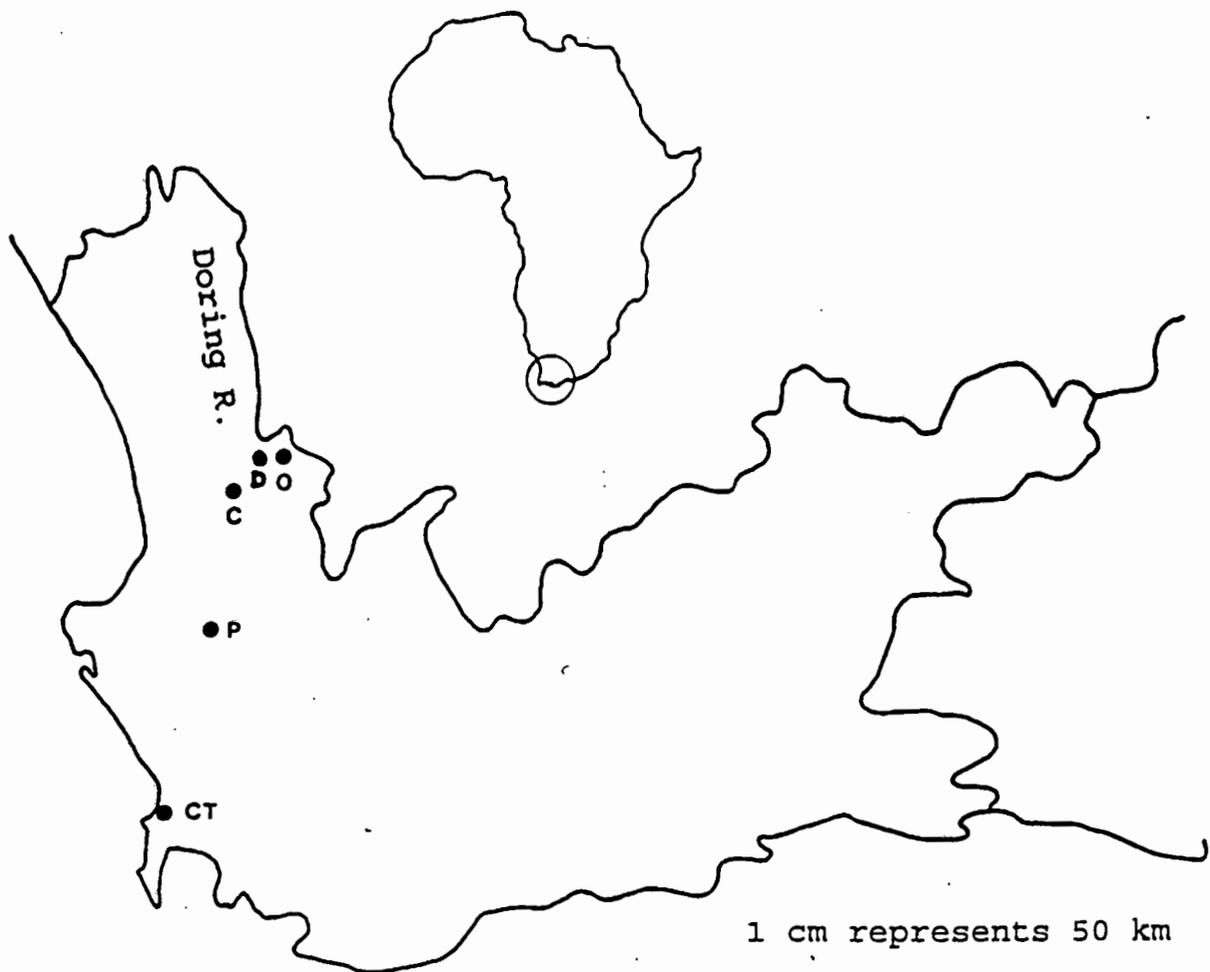
as all those that fell were consumed by livestock so pods were sampled from the trees only. None of the trees on Onderplaas farm retained pods so pods were collected from the ground only with the exception of one tree that retained its pods and which were harvested. Some pods were collected from the trees alongside the road between Onderplaas and Driefontein, but that were not fully ripe.

The pods on the ground were collected at random by throwing a pebble into the leaf litter below a tree and then placing a 25x25cm quadrat centrally onto the ground over the stone. The pods lying within and touching the quadrat were counted and collected and placed in a brown bag that was then stapled closed so that any emerging insects could not escape. Three such samples were taken from under each of the ten trees on sampling occasions. Where possible a similar number of pods were collected from each of ten trees. The differences in sample sizes were accounted for (see below). Only mature pods were collected from the trees as *N. arizonensis* lays eggs only on ripe pods whilst *A. prosopis* lays very few eggs on unripe pods (Hoffman, *pers. comm.*). The pods collected from between Onderplaas and Driefontein included many unripe pods to confirm that no eggs were being laid on "green" pods.

Each batch of pods was placed in a sealed, clear plastic container with a fine (0.1mm) gauze lid. These containers were housed in an insectory maintained at 27 $^+$/- 2°C with a 14 hour photo-period of lighting from florescent lamps. A sub-sample of 5 pods was kept aside and placed in a -20°C freezer for later observations. A further sub sample of 5 pods was taken to determine whether there was any parasitism of *A. prosopis* eggs. Any *N. arizonensis* eggs were removed before the pods were placed in a boiling tube sealed with fine gauze. The boxes were periodically (at 3-7 day intervals) checked for emerging bruchids or parasitoids. The respective number of *A. prosopis* and *N. arizonensis* was then recorded and the individuals transferred to a holding container for later be release. The larval parasites that emerged were preserved in 70% alcohol

for later identification. The bruchids and parasitoids that emerged within the tube were counted and included with the others within the box for general emergence. At the end of 35 days, the time required for the bruchids to complete development from eggs to adult (Zimmerman, 1991), the pods were discarded and replaced by pods collected from the subsequent samples so that emergence levels were observed for a 105day period.

The sample of five pods that were placed in the freezer was the smallest possible sample size found to be representative of the population with regard to numbers of eggs laid on the pods. These pods were then counted for the numbers of seeds present, the number of emergence holes in total, numbers of *N. arizonensis* eggs in total and the numbers of *N. arizonensis* eggs that were parasitised. These counts were done for each of the collection dates as well as a final count for the final emergence and parasitism levels on the last date that samples were considered.

The pods from each site were weighed at the end of the 35 days. The sample of five pods from each site was also weighed and the numbers of seeds in the pods was also counted to determine the number of seeds per gram of pods in each sample and this figure was used to determine the approximate number of seeds sampled on each occasion. Because the largest number of seeds in any one sample was found to be 3970 the respective numbers of emergence, parasite levels and egg numbers were then determined per 4000 seeds.

Data analysis

The total numbers of bruchids that emerged at each site was compared to determine the relative abundance of the two species throughout the sampling period. The

proportions of *N. arizonensis* and *A. prosopis* were compared for all sites combined and between the tree and ground samples for each site. The emergence of bruchids from the trees at Piketberg were only considered after the 16 April as the pods ripened late there and those initially obtained were unsuitable for the beetles.

Larval parasitism, having been standardised with regard to sample size, was then calculated to determine emergence over the sampling period for all sites. Egg parasitoids were abundant so comparisons between sites and situations (tree or ground) were possible. Because 'ground pods' are indistinguishable from recently fallen 'tree pods' it was assumed that eggs on the 'ground pods' were oviposited while these pods were on the ground. The effect of egg density on levels of parasitism by *Uscana* sp. was also determined by regressing percentage parasitism against egg numbers per pod.

Results

1) Emergence patterns of *A. prosopis* and *N. arizonensis*.

Between site comparisons are not valid because there were no ground pods at some sites and no tree pods at others, therefore all sites were lumped together and the respective graphs presented as such.

Considerably more *A. prosopis* emerged over the sample period than *N. arizonensis*, approximately 44000 to 10500 respectively (Fig. 2). Both species increased in numbers throughout the sampling period but rates of emergence were greatest early in the season and slowed with time.
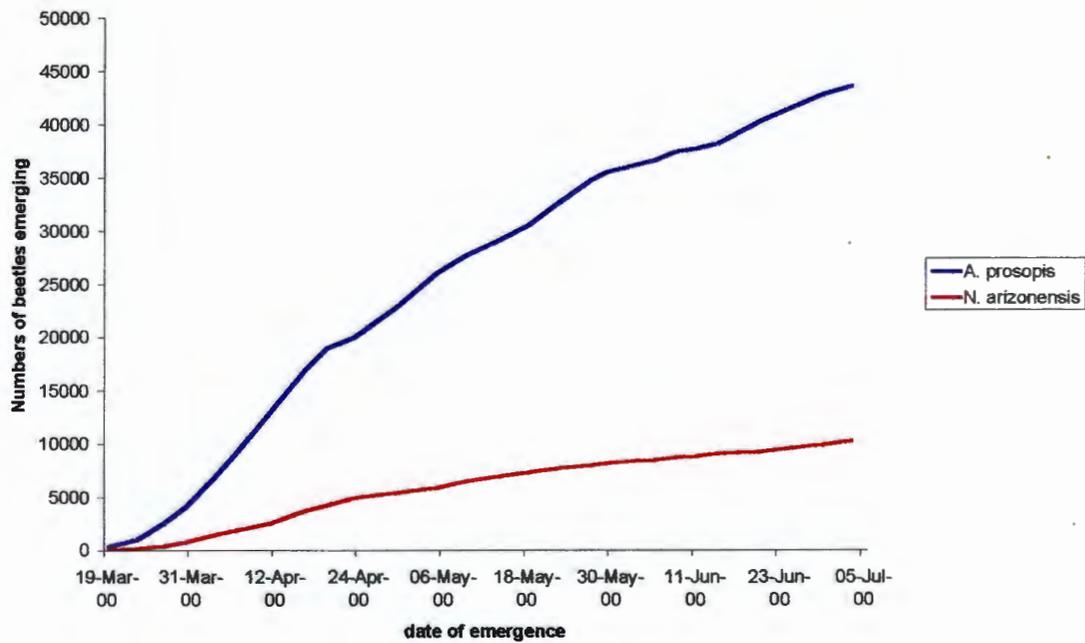
Fig.2: Cumulative emergence for all sites combines for *Algarobius prosopis* and *Neltumius arizonensis* over the entire sampling period.

Figure 3 shows percentage of beetles that were *N. arizonensis* throughout the sampling period. The proportion of *N. arizonensis* in the population was lowest during the first five weeks after which the proportions of the two species were constant. However *N. arizonensis* never exceeded more than 20% of the total. The proportional emergence numbers for the 'ground' and 'tree' pod samples is shown in Fig. 4. A far higher percentage of *N. arizonensis* emerged from the 'trees'
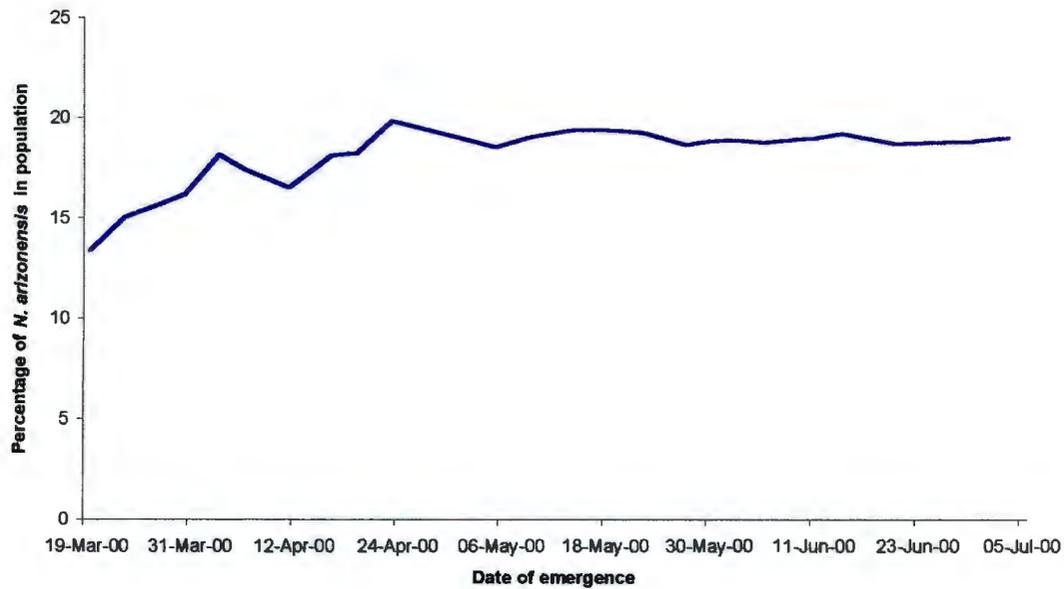
Fig. 3: Proportions of *N. arizonensis*: *A. prosopis* emerging over the entire sampling period for all sites combined.
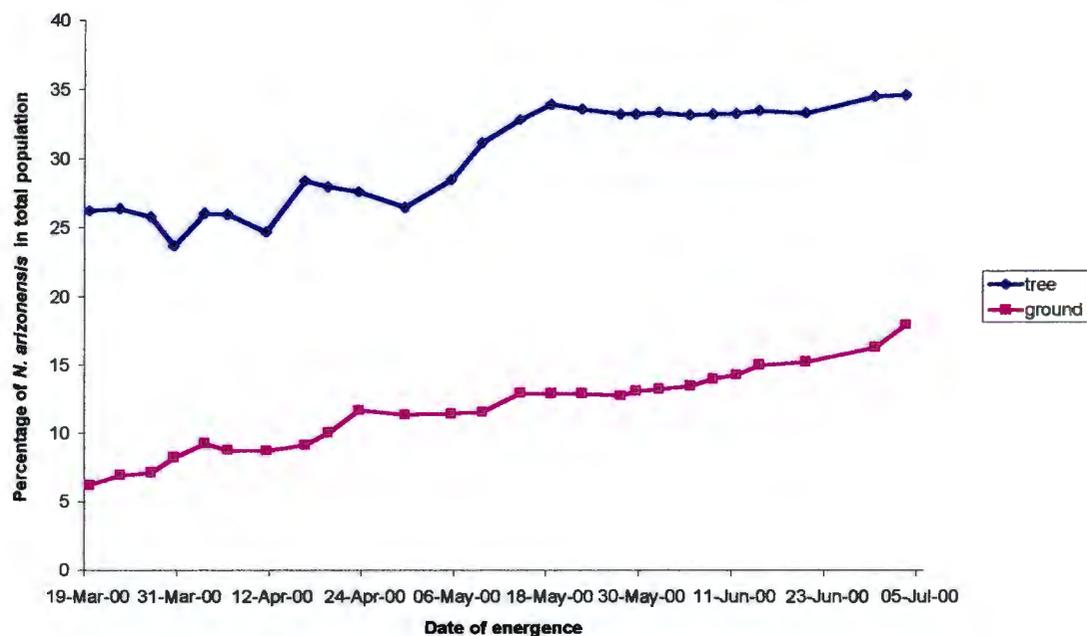

Fig. 4: Percentage of *N. arizonensis* emerging from 'tree' and 'ground' pods for all sites over the entire sampling period.

than from the 'ground' throughout the entire sampling period. The percentage of *N. arizonensis* increased for both the tree and ground samples as the season progressed.

The percentage of *N. arizonensis* that emerged from the 'trees' increased from approximately 26% to 33% where it stabilised for the remaining 6 weeks although fluctuations did occur over the first 6 weeks prior to the population stabilising. There was a constant increase in percentage emergence from the ground samples as the season went on, increasing from 6% to 18% at the end of the sampling period.

2) **Larval and pupal parasite emergence**

Several species of larval parasite emerged over the sampling period (Fig. 5). These were identified as representation of two families, Eupelmidae and Pteromalidae. The peaks on the graph are not representative of actual numbers because the sampling interval was set for the bruchid lifecycle and not for the parasitoids which have much shorter development times. The gaps between peaks reflect the short development stage of the larval parasites as most emerged within ten days of collection. Larval parasite numbers would therefore be higher if more frequent samples had been taken. The dotted line in Fig. 5 approximates larval parasite emergence had more samples been taken. However, if the larval parasitoid emergence is equated to beetle emergence over a shorter time period (ie. 7 days after the collection of the samples) then the three peaks translate to 4.4, 4.9 and 8.5% respectively of the total emergence of beetles and parasitoids over the same period. Larval parasitism was low at all sites in comparison to the total numbers of beetles emerging (Table 1). Additionally, it is unlikely that there was any difference in parasitism levels on *A. prosopis* compared with *N. arizonensis* and this form of parasitism was not considered further.
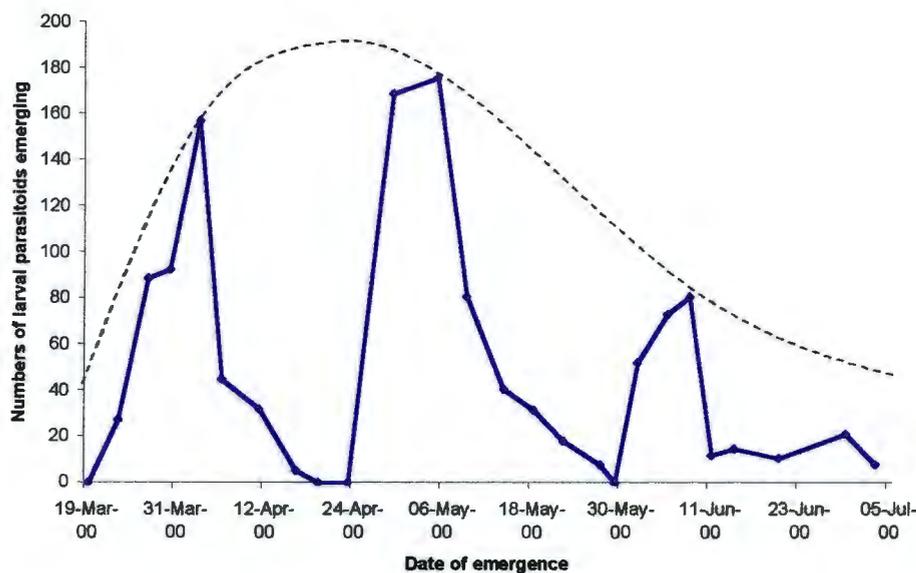
Fig. 5: Numbers of parasitoids that emerged for all sites over the sampling period. The dotted line represents the estimated emergence patterns for parasitoids had samples been collected more frequently from the field.

3) Egg parasitism on *N. arizonensis*

Egg parasitism, unlike larval parasitism, is assumed to affect *N. arizonensis* only and not *A. prosopis*. No egg parasitoids emerged from the pods devoid of *N. arizonensis* eggs and those that had an unspecified number of *A. prosopis* eggs only. Table 1 shows that *N. arizonensis* was affected more at some sites than others.

Table 1: Emergence figures for *N. arizonensis*, *A. prosopis* and larval parasitoids including levels of egg parasitoids for 'tree' and 'ground' pods

Species	Ground	Tree	Total
A.prosopis	29872	13898	43770
N.arizonensis	4796	5544	10340
larval parasitoids	407	835	1242
egg parasitoids	4359	31913	36272

Percentage egg parasitism for all sites combined was higher in the 'trees' than on the
ground (Figure 6), with egg parasitism in the 'trees' at increasing from 21% at the
start of the sampling to a maximum of 68% with the final sample. Egg parasitism
from 'ground' pods increases from 2% at the first sampling to a peak of 20% by the
third sampling and then dropped to 10 % by the end of the sampling period.

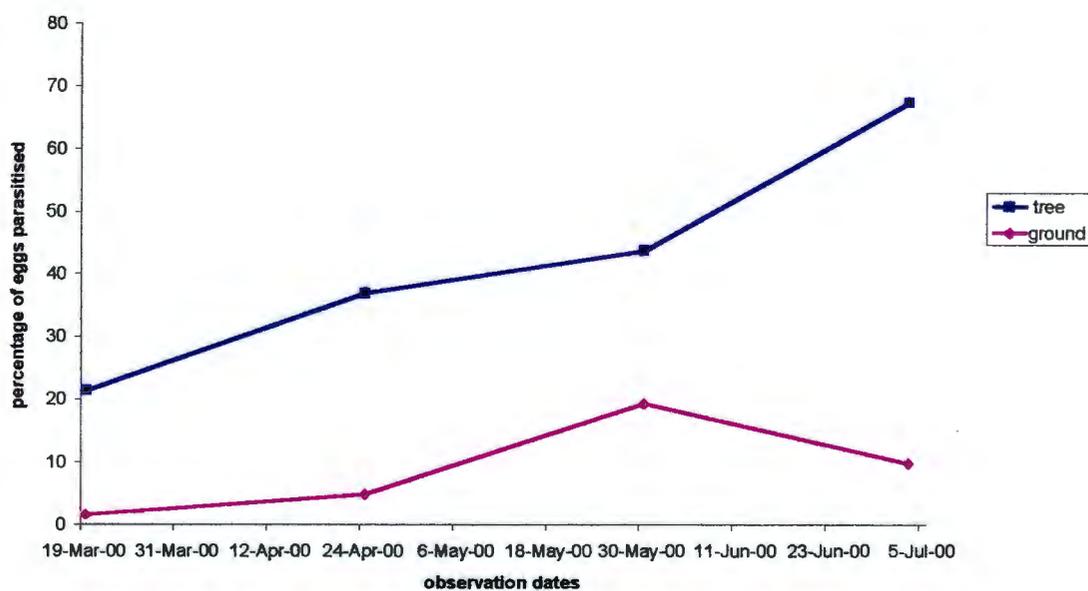Fig. 6: Percentage of *N. arizonensis* eggs parasitised by *Uscana* sp. at all sites
combined showing differences between 'ground' and 'tree' pods.

Percentage parasitism was regressed against number of eggs per pod firstly for all
sites and for 'ground' and 'tree' positions separately at each of the sites. The
regression showed no significant relationship between levels of parasitism and egg
numbers (Table 2).

Table 2: R^2 values for correlations between levels of egg parasitism and egg density at the different sites for the entire sampling period.

Site	Position	R^2 value
all sites	t and g	0.069
Clanwilliam	ground	0.019
	tree	0.001
Driefontein	tree	0.07
Onderplaas	ground	0.001
	tree	0.145
Piketberg	ground	0.165
	tree	0.07

Discussion

1) Emergence patterns of *A. prosopis* and *N. arizonensis*.

Failure of *Algarobius bottimeri* to establish and reduction in effectiveness of *A. prosopis* in destroying seeds of *Prosopis* plants due to their inability to survive through the digestive tract of livestock (Zimmerman, 1991), resulted in the introduction of *Neltumius arizonensis* to South Africa (Moran *et al*, 1993). Previous work found *N. arizonensis* to lay eggs on unripe pods (Swier, 1974 as cited in Moran, 1991) resulting in destruction of the seeds by beetles prior to ingestion by livestock and Moran (1991) concluded that *N. arizonensis* could be a promising biocontrol agent to complement *A. prosopis*. However, it was later discovered that *N. arizonensis* only laid eggs on ripe pods (Impson *et al*, 1999). Strathie (1995 unpublished) proposed that because *A. prosopis* had established itself successfully and over a wide range, the potential existed for competition between the two species. *N. arizonensis* was deemed to be "competitively equivalent" to *A. bottimeri* (Strathie,

1995 unpublished) which had failed to establish possibly because it was out-competed by *A. prosopis*. There was concern was that *A. prosopis* had established populations and was known to be a better competitor than *N. arizonensis*, aggressively killing *N. arizonensis* when coming into contact with this species (Hoffman, *pers. comm.*). Not only was there likely to be strong competition but the egg laying strategy of *N. arizonensis* exposes the eggs to parasitoids more so than the concealed eggs of *A. prosopis*. The answer to why *N. arizonensis* has managed to persist in the face of such adversity could lie in life-history strategies. It is possible that N. arizonensis could lay an excess of eggs, thereby increasing fecundity and the chance of larvae successfully developing through to adulthood. This is however not the case as *N. arizonensis* lays only 80 eggs over a 35 day period compared to *A. prosopis* that lays, on average, 200 eggs over a similar period (Strathie, 1995 unpublished). *N. arizonensis* minimises both intra and interspecific competition by careful inspection of the pod and laying eggs only above those seeds that do not already have an egg on them (Strathie, 1995 unpublished). This strategy results in reduced competition with conspecifics but may not reduce competition with the larvae of *A. prosopis* whose eggs are concealed in crevices and emergence holes and whose larvae are far more mobile than those of *N. arizonensis* (Swier, 1974 as cited in Strathie, 1995 unpublished).

An alternative strategy employed by *N. arizonensis* might be that of resource partitioning with possible variation in population numbers at a temporal scale so as to reduce the overlap with *A. prosopis*. This was one of the driving questions this paper aimed to answer. Emergence of both species was considered over the sampling period for all sites to see if there was a levelling off in the populations of *A.prosopis* at particular times and an increase in *N. arizonensis* numbers coinciding with these

periods. This would help to explain the persistence of *N. arizonensis* populations due to an increase in resource availability. However, this is not the case, and constant increases in both species through the sampling period were found (Fig. 2). Both species had low levels of emergence for the first week but this increased rapidly over weeks 2 and 3 before slowing down to a constant rate of emergence. *N. arizonensis* numbers for the combined sites were always very low and were never more than 20%, levelling off for the majority of the season at approximately 19%. The slower start by *N. arizonensis* might be owing to a poorer ability of the species to over-winter. Kistler (1985) found that *A. prosopis* is better adapted in terms of reproductive and physiological processes to deal with extreme temperatures that coincide with peak pod production than is *N. arizonensis* is. This would enable larger numbers of *A. prosopis* to survive through the period of minimal to zero pod production and then re-establish and rapidly increase in numbers with the first production of pods in the new season (Fig.'s 2 and 3). The ability of *A. prosopis* to lay on green pods (Swier, 1974 as cited in Moran, 1991) in conjunction with high numbers at the start of the season effectively reduces the resources available to *N. arizonensis*.

The next question to consider is whether *N. arizonensis* shows preference for 'ground' or 'tree' pods thus partitioning resources on a spatial scale. Figure 4 shows the differing proportions of *N. arizonensis* in the 'tree' and 'ground' pods. Throughout the season there was a far higher percentage of *N. arizonensis* emerging from the 'trees' than from the 'ground' reflecting either a preference for laying in 'trees' by *N. arizonensis*, or a preference by *A. prosopis* for laying on the 'ground'. Table 1 shows the numbers of *A. prosopis* and *N. arizonensis* emerging from 'ground' and 'tree' pods. *Algarobius prosopis* shows preference to laying eggs on 'ground' pods and *N. arizonensis* on 'tree' pods. These results reflect and confirm those obtained by

Coetzer (1996, unpublished), that *N. arizonensis* prefers to lay on 'tree' pods rather

than 'ground' pods. At the start of the season mature 'tree' pods were limiting and

thus possible sites for *N. arizonensis* to lay eggs on were fewer than those available to

A. prosopis that are able to lay on unripe pods. Because of this, *N. arizonensis* may

have been forced to lay on 'ground' pods thus explaining the difference in

percentages of seeds parasitised on 'ground' and 'tree' pods in Fig. 7.
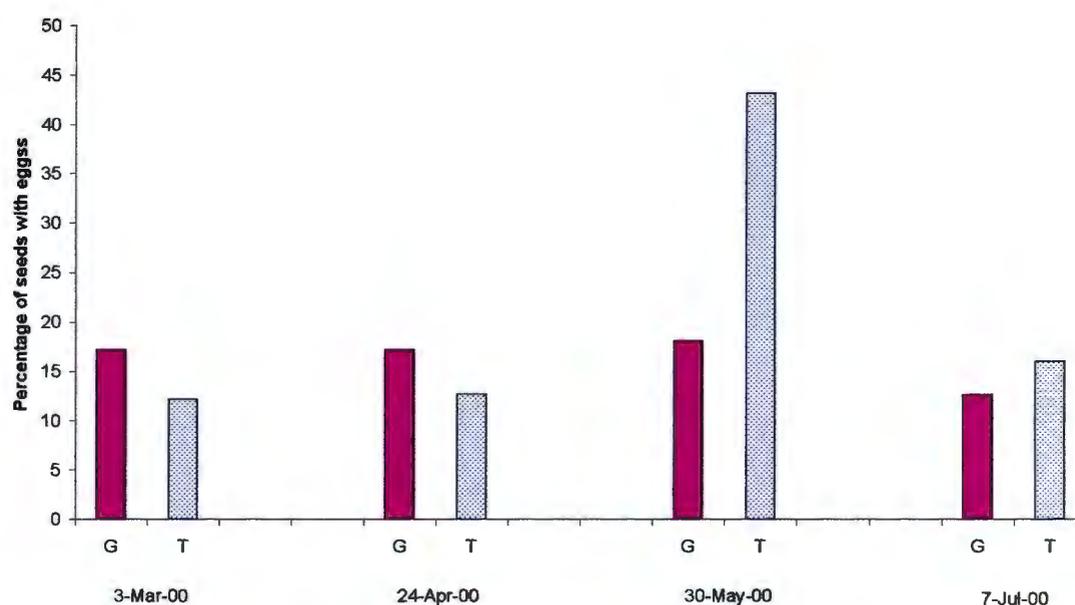

Fig. 7: Percentage of seeds with *N. arizonensis* eggs from 'ground' (G) and
'tree' (T) positions over the four observation times.

As the season progressed so too did the numbers of ripe pods occurring within the

trees and hence the sudden increase in percentage of seeds with eggs on 'tree' pods.

This also goes towards explaining the fluctuations in emergence percentages of *N.*

arizonensis at the start of the sampling period (Fig. 4).

2) Larval and pupal parasite emergence

The differences in numbers observed between the two bruchid species cannot be explained only on the basis of where each species lays its eggs. If anything, it confuses the issue, as by demonstrating that *N. arizonensis* and *A. prosopis* are partitioning their resources spatially, one would assume that their emergence numbers would be more similar. The next step is to determine if there are other factors resulting in low emergence of *N. arizonensis* relative to the emergence numbers of *A. prosopis*. Hoffman *et al.* (1992) discovered *A. prosopis* was host to 10 species of indigenous parasitoid wasps. In their study, the highest level of parasitism found was 5.3% from any one sample this lead the authors to conclude that at these levels, larval and pupal parasitoids would not hinder *A. prosopis*' biocontrol effectiveness. The highest peak in larval parasitoid emergence found in the current study was equivalent to 8.5% of the bruchid emergence over the same period. The estimated parasitoid levels, indicated as a dotted line (Fig. 5), do not describe high parasitism levels. It seems unlikely that larval parasitism has any significant effect on the bruchid populations and is presumed to affect both species of bruchid equally. Therefore, difference in emergence numbers of the two species cannot be explained by larval parasitism.

3) Egg parasitism on *N. arizonensis*

Egg parasitism of N. arizonensis was very high over the sampling period with 3.5 times more eggs parasitised than there were N. arizonensis emerging (Table 1). In the absence of egg parasitoids and assuming 100% survivorship of offspring, *N. arizonensis* would have resulted in emergence numbers equalling those of *A. prosopis*. Figure 6 shows that 'tree' eggs are parasitised to a far greater extent than are 'ground' eggs, 68% to 19% respectively at their maximum levels of parasitism.

Coetzer (1996, unpublished) found varying levels of egg parasitism from 0% parasitism up to 63% parasitism, from samples collected toward the end of September. Egg parasitism on 'ground' pods drops off after peaking in May. This might be the result of increasing levels of fungus associated with 'ground' pods as the rainy season commences, because *N. arizonensis* prefers to oviposit on pods that do not harbour fungus (Coetzer, 1996 unpublished).

As the season progresses so egg parasitism increases, in tandem with the densities of *N. arizonensis* eggs. Table 2 shows that percentage parasitism and egg number are not significantly correlated for any site and thus we can assume that there are equal chances of parasitism for those eggs on the 'ground' pods and those eggs on the 'tree' pods regardless of the densities of the eggs present. *Uscana* sp. are not therefore targeting 'tree' eggs because they attain higher densities but because they are the preferred position for parasitising bruchid eggs.

4) Alternative means of biocontrol

The initial concern by farmers with the biocontrol programmes was the loss of a resource that benefitted both livestock and humans, hence the introduction of seed feeding bruchids that do not detract from the plants usefulness. However, it is now apparent to researchers and farmers alike that the costs, both economic and environmental, far outweigh the benefits of the plants and it is time to introduce other forms of biocontrol agents (Coetzer, 1996 unpublished).

Hoffman and Moran (1992) reported that fecundity of the introduced weed *Sesbania punicea* was reduced by 99.6% by the seed-feeding curculionid, *Rhyssomatus marginatus* when feeding alongside the bud feeding *Trichapion lativentre*. Rogers (1976) and Moran (1991) describe a host of species that inflict considerable damage upon the buds of *Prosopis*. If a bud feeding insect were introduced to compliment the

damage caused to seeds by *A. prosopis* and *N. arizonensis*, *Prosopis*' fecundity might be reduced to sufficient levels to slow its rate of spread. However, a concern here is the affect on the extensive apiculture industry that has been established around these prolifically flowering plants.

Plants with different life histories employ different methods of survival and dispersal. Short-lived plants tend to produce rely on vast quantities of seed in order for the maintenance of their gene-line but long-lived plants rely more on survivorship with less emphasis on fecundity. Golubov *et al* (1999), having applied elasticity matrices to *P. glandulosa* populations, found that fecundity plays a very minor role in persistence and expansion of *Prosopis* populations into grasslands in southern United States. It was found that in fact stasis in one life stage contributed the most to continuance of populations of these long-lived trees. It is therefore likely that the best means of eradicating *Prosopis* would be to destroy the plants through the use of defoliating or stem boring insects rather than by reducing fecundity. Because of the importance of *Prosopis* as both a shade plant and a source of firewood, the effect of stem borers and defoliators on adult trees it is still of concern to farmers. It would therefore be advantageous if insects were introduced to attack only seedlings and young plants so as to maintain the adult plants. Weltzin et al (1998) found that *Prosopis* seedlings have a 75% survivorship even after several clippings. Therefore it seems unlikely that defoliators that attacked only seedlings would be effective. The solution to the *Prosopis* problem might therefore be one of adult and young plant destruction through the introduction of either defoliators or stem borers. This demonstrates the importance of research into an 'invasives' life history and into indigenous parasitoids prior to the implementation of a biocontrol programme.

Conclusions

There are large differences between numbers of the two bruchid species emerging from the different sites with a definite preference shown by *N. arizonensis* to lay in 'tree' pods. However, the egg parasitoid, *Uscana* sp., also shows a preference for parasitising eggs in 'tree' pods over those on the 'ground' pods. The conclusion that Coetzer (1995, unpublished) made, that *Uscana* sp. does not affect the effectiveness of *N. arizonensis* as a biocontrol agent was premature. This study has shown that *Uscana* sp. affects *N. arizonensis* effectiveness by reducing their emergence numbers dramatically. It seems unlikely that *N. arizonensis* and *A. prosopis* are able to reduce the rate of spread of *Prosopis* species and introduction of additional biocontrol agents seems the likely answer to curbing the expansion of *Prosopis*' range in Southern Africa.

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