NELTUMIUS ARIZONENSIS (SCHAEFFER) (COLEOPTERA: BRUCHIDAE) AS A BIOLOGICAL CONTROL AGENT OF MESQUITE (*PROSOPIS* SPP., MIMOSACEAE) IN SOUTH AFRICA

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CONTENTS

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ABSTRACT

In the late nineteenth century, six North American mesquite taxa (*Prosopis* spp., Mimosaceae) were introduced into South Africa. They were to provide shade for livestock, and their pods were valued as a source of fodder. All *Prosopis* species in South Africa were recognized as weeds in 1983. In 1987 a biological control programme using seed weevils (Coleoptera: Bruchidae) was launched against the two most invasive taxa, namely, *P. glandulosa* var. *torreyana* (L. Benson) M.C. Johnston and *P. velutina* Wooton.

Algarobius prosopis (LeConte), the first biocontrol agent released, destroys large numbers of mesquite seeds annually, where livestock do not graze pods that are lying on the ground. Where pods are grazed, however, there is insufficient time for *A. prosopis* to inflict an adequate degree of seed damage before pods are eaten. For this reason another bruchid, *Neltumius arizonensis* (Schaeffer), which was reported to be capable of ovipositing on immature and mature tree-borne pods, was released in 1993.

The establishment of *N. arizonensis* on mesquite at three sites in Western Cape Province was confirmed by monitoring *N. arizonensis* oviposition and emergence in the field. High levels of oviposition by *N. arizonensis* on tree-borne pods in June 1994 (39% and 29% 'egg-seeds' at Onderplaas and Clanwilliam, respectively) were accompanied by high rates of trichogrammatid egg parasitism. Most pods had fallen to the ground by this time. The degree of egg parasitism was independent of *N. arizonensis* egg density. From December 1994 until June 1995, *N. arizonensis* egg densities were lower than those recorded in June 1994. The rate of field oviposition by *N. arizonensis* returned to high levels in August and September 1995, when 'tree pods' were again few in number. *Neltumius arizonensis* eggs were more abundant on 'tree pods' than on 'ground pods' in August and September 1995.

In a laboratory experiment, *N. arizonensis* females preferred to oviposit on pod-segments that were free of fungal hyphae, when

offered a choice of these, and pod-segments infested with fungal growth. This observation, together with observations of mesquite pod phenology, led to the proposal of a model that explained the pattern of *N. arizonensis* oviposition in the field: In winter and spring, when pods without fungus are scarce and restricted to tree branches, and while 'ground pods' are fungus-infested, *N. arizonensis* females target mainly 'tree pods'. At this time *N. arizonensis* eggs are common on 'tree pods'. In summer, when fungus-free pods are abundant before winter rain has enabled fungal growth on them, very few *N. arizonensis* eggs are to be found. Variation in field *N. arizonensis* oviposition levels could therefore be a function of the availability of 'clean' pods that are not infested with fungus, and not an indication of changes in *N. arizonensis* population size.

Monitoring of seasonal abundance of *A. prosopis* provided a measure against which the success of *N. arizonensis* could be judged. Monthly monitoring of the number of bruchid-damaged mesquite seeds gave an indication of the success of the introduced bruchids to date. Overall, *A. prosopis* emerged twenty times more frequently than *N. arizonensis*, and therefore accounted for the vast majority of damaged seeds. This could be a result of the earlier release of *A. prosopis* in the field, compared to that of *N. arizonensis*. Together, both species destroyed 69% and 55% of seeds at two livestock-free sites in 12 months, and 38% of seeds in six months at a site frequented by goats.

The likelihood of *N. arizonensis* becoming a successful mesquite biocontrol agent is discussed. It is predicted that *N. arizonensis* will probably not be as effective as *A. prosopis*. The theoretical basis for using seed-feeding insects in weed biocontrol is explored, and selected biocontrol programmes that have employed seed-feeders are discussed. Prospects for the introduction of other phytophagous insects for mesquite biocontrol in South Africa are examined.

CHAPTER 1: GENERAL INTRODUCTION

1) Mesquite in its land of origin

Mesquites, or plants of the genus, *Prosopis* (Mimosaceae) are thorny shrubs or trees that are distinguished from other mimosoid genera by their fleshy, indehiscent seed pods (Figure 1.1, Plate 1). The centre of speciation and ecological diversification of the genus extends across Argentina, Chile and Paraguay, and thirty-one *Prosopis* species are indigenous to South America (Fagg and Stewart, 1994). Only three species occur in Asia, and one species is restricted to Africa. Nine *Prosopis* species are native to Mexico and the southern United States of America (USA), and this region is considered to be the secondary centre of diversity of the genus (Fagg and Stewart, 1994). While certain mesquites have been distributed worldwide for use in afforestation programmes, they have also become serious weeds of agriculture in their native and exotic habitats (DeLoach, 1984).

2) Mesquite in South Africa

Five mesquite taxa have become naturalized in South Africa (Harding, 1987). They are: *Prosopis chilensis* (Molina) Stuntz, *P. glandulosa* var. *glandulosa* J. Torrey, *P. glandulosa* var. *torreyana* (L. Benson) M.C. Johnston, *P. juliflora* (Swartz) DC, *P. pubescens* Bentham and *P. velutina* Wooton. Considerable confusion prevails regarding the taxonomy of mesquite in South Africa, because plant phenotypes vary according to climatic conditions, and because certain species hybridize readily (Harding, 1987; Zimmermann, 1991). It is agreed, however, that while *P. chilensis* and *P. pubescens* are not weeds in South Africa, *P. glandulosa*, *P. juliflora* and *P. velutina* are strongly invasive in this country. Although *P. glandulosa* var. *torreyana* and *P. velutina* have the worst reputations, all *Prosopis* species in South Africa are declared invaders under the Conservation of Natural Resources Act 43 of 1983 (Zimmermann, 1991).

Prosopis glandulosa var. *torreyana* was first introduced into South Africa from its native USA in 1880 (Alston, 1914 cited by

Figure 1.1 Flowering shoots (a) and mature pods (b) of *Prosopis glandulosa* var. *torreyana* (drawn by G. Condy, reproduced from Zimmermann, 1991).

Plate 1 Pod-laden mesquite tree

Zimmermann, 1991). Infestations of mesquite grew rapidly after further importations of seed, and because the plant's propagation was encouraged by the Departments of Agriculture and Forestry. In South Africa the most dense infestations of mesquite are found in the north-western Karoo region, particularly in the districts, Carnarvon, Kenhardt, Prieska and Williston (Vorster, 1985). Mesquite is also encountered in Namibia and Botswana. In 1989 approximately 180 400 ha in Northern Cape and Western Cape were mesquite-infested, and it was estimated that the total land area susceptible to mesquite invasion may be as large as 930 000 ha (Harding and Bate, 1991).

3) Beneficial attributes of mesquite

Mesquite may be exploited by man and animals in various ways (DeLoach, 1984; Harding, 1987; Poynton, 1990; Fagg and Stewart, 1994). In the late nineteenth century, the prospective use of its pods for livestock fodder, and its provision of shade to animals, were the reasons for its introduction into South Africa. In North Africa and Asia, livestock fodder is sought in the browse of the indigenous *Prosopis* species, and not in the pods, which are used as a fish poison in Sudan. In the Americas the opposite is true: while pods of New World mesquites are highly valued as nutritious fodder, leaves of these species are usually unpalatable to livestock. The wood of large trees has potential for use as timber (Fagg and Stewart, 1994). Although small trees are unsuitable for timber production, their wood may be used for fence droppers, furniture, firewood and charcoal. Though apparently not well developed in South Africa, the extraction of tannins and gums from mesquite is practised in North America. In South America, mesquite pods are used to make bread and alcoholic beverages, and honey made by bees foraging on mesquite flowers is reported to be of good quality (Fagg and Stewart, 1994).

South African proponents of mesquite agroforestry cite the above uses, and the fact that mesquite is tolerant of drought and alkaline and saline soils, when countering the weed's condemnation (Poynton, 1990). Although the value of *P. chilensis*

as a shade tree in South Africa remains undisputed, the use of mesquite pods as livestock fodder is not as common today as it was in the past, for farmers fear the exacerbation of mesquite infestations on their land (Harding, 1987; Zimmermann, 1991).

4) Deleterious effects of mesquite

Sheep may destroy up to 85% of mesquite seeds they eat. Undamaged seeds that are scarified in sheep intestinal tracts, and passed with their dung to germinate readily, far out-number those needed by mesquite infestations to spread (Harding, 1991). The efficacy of sheep in destroying ingested seeds, however, has been shown to decrease over a period of three weeks of continuous feeding (Harding, 1991). The inhibitory effect of sugars in mesquite pods on the digestive systems of cattle renders them less capable in destroying seeds than sheep (Felker, 1979 cited by Harding, 1991), and causes intestinal blockage in cases of overfeeding (Poynton, 1990). The above facts, in conjunction with mesquite's prolific seeding, mean that the weed is an aggressive invader of grazing farmland (Harding, 1987; Zimmermann, 1991).

In the USA, the loss of 200 to 500 million dollars annually in the livestock industry is due to the invasion of grazing land by mesquite. Grasses are out-competed by the weed for space and water, and when infestations become very dense, trees block the passage of livestock animals, increasing the cost of animal mustering (DeLoach, 1984). Mesquite must have the same effect in South Africa, although published, quantitative studies on its effect here are uncommon, unlike those on other woody, perennial weeds such as Australian acacias and pines (see Versveld and van Wilgen, 1986). That mesquite out-competes indigenous plants, possibly for water, was demonstrated by Vinjevold, Bridgeford and Yeaton, 1985, cited by Brown and Gubb, 1986). The cost of chemical and mechanical control, which are ineffective, is often higher than the value of mesquite-infested land. Biological control along with intensive utilization seems to be the only viable alternative for the integrated management of mesquite in South Africa (Zimmermann, 1991).

Algarobius bottimeri did not establish.

to Acocks (1988), Succulent Karoo vegetation grows in the undisturbed low-lying parts, and the nearby Cederberg range of mountains harbours Fynbos vegetation.

Piketberg site (32°57'S ; 18°46'E, "P" on map) lies five km South of Piketberg town, adjacent to the national road from Cape Town. Small patches of what Acocks (1988) called Coastal Renosterveld punctuate the region's vast wheat-belt, which is elevated less than 300m above sea level. At the nearby town of Porterville, an average of 324mm of rain fell per year, over the last five years. In 1994, total monthly rainfall at Clanwilliam and Piketberg was highest in the month of June (South African Weather Bureau, Pretoria).

Both *A. prosopis* and *N. arizonensis* were released at Onderplaas. The former species was released by farmers on numerous farms in the north-western Cape during April 1989 (see Zimmermann, 1991). The latter species was released at Onderplaas on four occasions (J.H. Hoffmann, University of Cape Town, pers. comm.): On 02/12/1993 about 5 000 *N. arizonensis* adults were released, and on 20/12/1993, 20/1/1994 and 4/3/1994, about 3 000, 9 000 and 800 *N. arizonensis* adults were released, respectively.

Both *A. prosopis* and *N. arizonensis* were released at Clanwilliam and Piketberg (Zimmermann, 1991; J.H. Hoffmann, University of Cape Town, pers. comm.). On 11/08/1993 about 3 000 *N. arizonensis* adults were released at Piketberg, and on 26/10/1993 about 2 000 *N. arizonensis* adults were released at Clanwilliam.

7) Aims and scope

The primary aim of this investigation was to confirm the establishment of *N. arizonensis* on mesquite, and to report on the biocontrol effectiveness of *N. arizonensis*, in comparison to that of *A. prosopis*, at three sites in South Africa's Western Cape Province. Chapter 2 is a quantitative account of the oviposition of *N. arizonensis* females in the field, and of the parasitism of *N. arizonensis* eggs by Trichogrammatidae. Chapter 3 treats the

seasonal emergence of *A. prosopis* and *N. arizonensis*, the number of mesquite seeds damaged by them, and the incidence of parasitism of bruchid larvae and pupae. The particular aims of chapters 2 and 3 are outlined at the beginning of those sections. In Chapter 4, a discussion relating the results of this study, and those of others, to the concept of biological control of perennial weeds using seed-feeders, is presented. The question of which additional mesquite biocontrol agents should be introduced, is then explored.

8) Glossary of terms

'seed': When printed in inverted commas, this word refers to one of the successive exocarp swellings along the length of the pod, within which the small, hard, brown mesquite propagule is contained. When inverted commas are not present, **seed** refers to the small, hard, brown mesquite propagule.
'egg-seed' refers to a 'seed' onto which a *N. arizonensis* egg has been oviposited.

'clean pod' refers to the fungus-free state of a mesquite pod.
'fungus pod' refers to the fungus-infested state of a mesquite pod.

'tree pods' are pods that are still tree-borne, and have not yet fallen to the ground.
'ground pods' are abscised pods that have fallen from trees and are lying on the ground.

CHAPTER 2: *NELTUMIUS ARIZONENSIS* EGG DENSITY AND PARASITISM OF *N. ARIZONENSIS* EGGS BY TRICHOGRAMMATIDAE

SUMMARY

Part I of the following chapter reports on the seasonal density of *N. arizonensis* eggs in the field, and the rate of parasitism of these eggs by *Uscana* sp. (Trichogrammatidae). In part II, the oviposition-site ('ground pods' or 'tree pods') preferences of *N. arizonensis* and *Uscana* sp. are tested using data from monthly pod collections, and from the field experiments. The relationship between *N. arizonensis* egg density and the degree of egg parasitism by *Uscana* sp. is examined in part III. Part IV recounts a laboratory experiment that tested whether the propensity of *N. arizonensis* to lay eggs is stronger on pods that are free of fungus, than on fungus-covered pods.

A model of the phenology of *N. arizonensis* oviposition is presented. The model is based on results of the monitoring study and the laboratory experiment.

PART I: FIELD MONITORING OF *N. ARIZONENSIS* EGG DENSITY, AND PARASITISM OF ITS EGGS BY *USCANA* SP.

AIMS

The objectives of the work reported here were to: 1) confirm that *N. arizonensis* had established at the three field sites at which it was released, namely, Onderplaas, Clanwilliam and Piketberg, by monitoring the seasonal density of eggs, and 2) measure the degree of parasitism of *N. arizonensis* eggs by *Uscana* sp.

METHODS

On 3 June 1994, 'tree pods' were picked from one tree at Clanwilliam and three trees at Onderplaas for the purpose of quantifying *N. arizonensis* egg density, and parasitism of *N. arizonensis* eggs by trichogrammatid wasps. 'Ground pods' were not collected in June 1994, and 'tree pods' were not available at Piketberg at this time. On nine sampling occasions from 1 December 1994, when 'tree pods' were green and immature, until 5 September 1995, when most pods had fallen, 'tree pods' and 'ground pods' were examined for the presence of unparasitized and parasitized *N. arizonensis* eggs. Table 3.1 (chapter 3) contains the dates on which pod collections took place.

Neltumius arizonensis egg densities on 'ground pods' were compared with those on 'tree pods'. Because the separation of 'ground pods' and recently-fallen 'tree pods' presented practical difficulties, it was assumed that eggs on 'ground pods' were oviposited while these pods were on the ground.

RESULTS

June 1994

In June 1994, *N. arizonensis* females oviposited on 29% of 'seeds' on 'tree pods' at Clanwilliam (from one tree, n = 367 'seeds'), and 39% of 'seeds' on 'tree pods' at Onderplaas (from three trees, n = 818 'seeds') (Figure 2.1). Thirty-five per cent and 53% of the eggs at Clanwilliam (n = 107 eggs) and Onderplaas (n = 317 eggs), respectively, had been parasitized by trichogrammatid wasps (Figure 2.1). These trichogrammatids were identified as *Uscana* sp., a small cosmopolitan Genus that is apparently host-specific on the eggs of bruchid beetles (G.H. Prinsloo, Plant Protection Research Institute, South Africa, pers. comm.).

January 1995 until June 1995

Egg-count data from 'tree pods' and 'ground pods' were combined after June 1994. From January 1995 until the end of June 1995 at all three sites, monthly *N. arizonensis* egg densities on 'ground pods' plus 'tree pods' were lower than those recorded on 'tree pods' alone in June 1994 (Figure 2.1). No eggs were found on the green, immature pods sampled on 01/12/1994. At Clanwilliam, the frequency of 'egg-seeds' remained below 1% from January until June 1995, during which time about 15 000 'seeds' from that site were examined. At Piketberg, *N. arizonensis* egg density increased from 1.2% 'egg-seeds' in March 1995 (n = 2124 'seeds') to 7.3% 'egg-seeds' in May 1995 (n = 2312 'seeds'). At Onderplaas, *N. arizonensis* females had oviposited on 5.4% of the 'seeds' examined in April (n = 2322 'seeds'). One-hundred and seventy-two eggs of 316 eggs (54.4%) collected at Onderplaas from 18/01/1995 until 29/06/1995 had been parasitized by trichogrammatid wasps (Figure 2.1). On pods collected between the same dates, not one of the 66 eggs found at Clanwilliam was parasitized, and none of the 354 eggs retrieved from Piketberg was parasitized.

FIGURE 2.1 The occurrence of *N. arizonensis* eggs in monthly pod samples, and the frequency of parasitized eggs (filled portions of bars). Numbers above bars indicate the numbers of eggs found. C = Clanwilliam, O = Onderplaas, P = Piketberg.

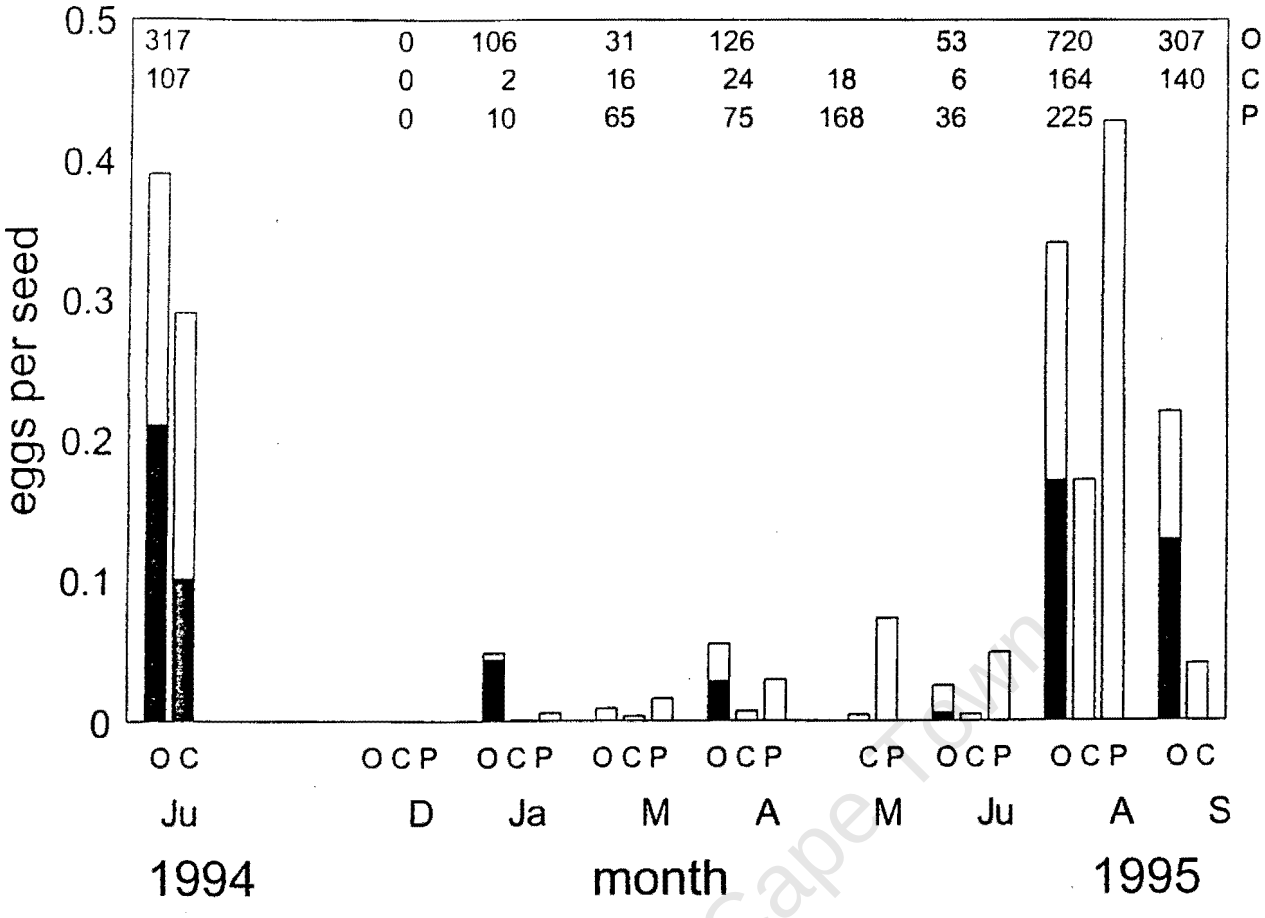
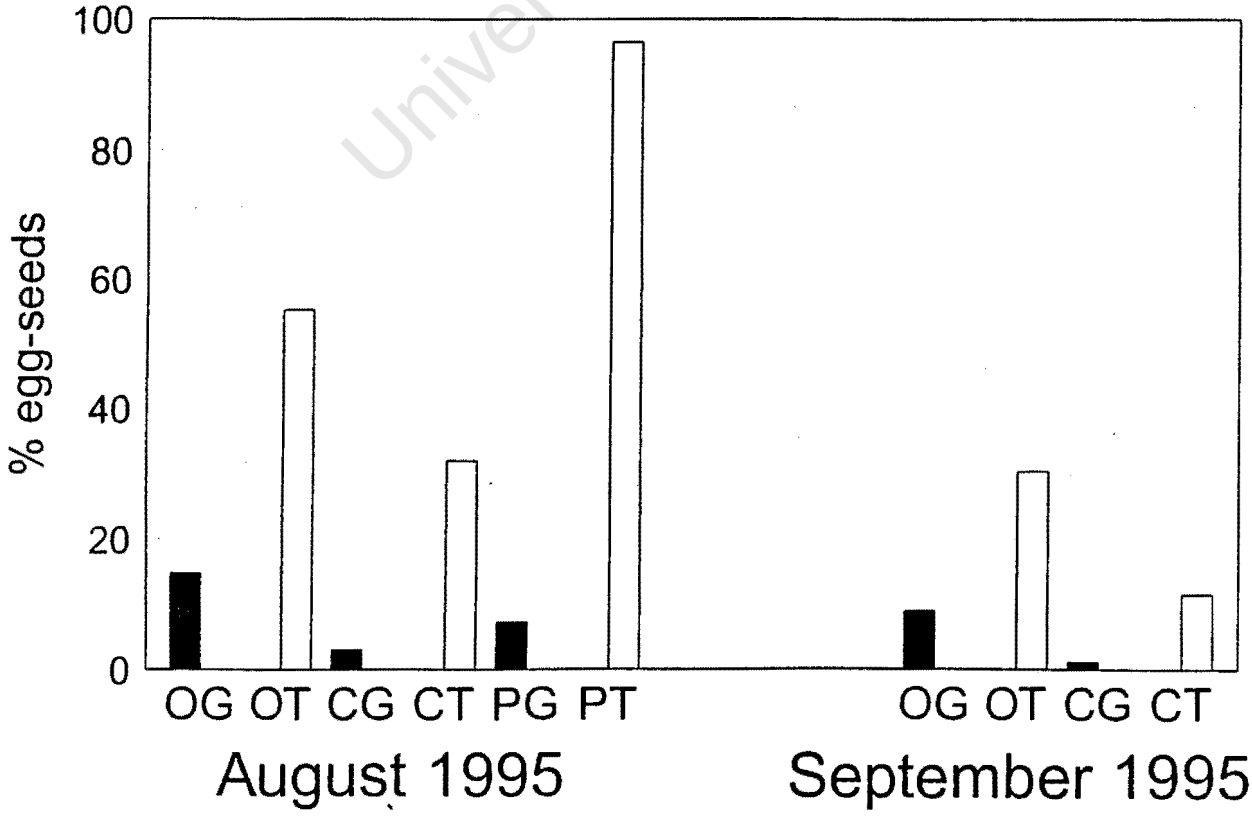


FIGURE 2.2 Percentage 'egg-seeds' on 'tree pods' compared to percentage 'egg-seeds' on 'ground pods', in August and September 1995. C = Clanwilliam, O = Onderplaas, P = Piketberg. G = ground, T = tree. Filled bars represent 'ground pod' data; unfilled bars represent 'tree pod' data.



August and September 1995

In August 1995 the percentage 'egg-seeds' increased dramatically at Clanwilliam (17%), Onderplaas (34%) and Piketberg (43%) (Figure 2.1). A high density of *N. arizonensis* eggs was maintained at Onderplaas in September 1995 (22%), and in comparison with the density of eggs at Clanwilliam in the months preceding August, *N. arizonensis* eggs were also relatively numerous there in September 1995 (4%). No 'tree pods' were available at Piketberg in September 1995. The rate of trichogrammatid parasitism was 50.4% at Onderplaas in August 1995, and 58.3% at that site in September 1995 (Figure 2.1). None of the eggs retrieved from Clanwilliam in August and September 1995 was parasitized, and none of the eggs from Piketberg in August 1995 was parasitized.

Figure 2.2 compares the frequencies of *N. arizonensis* eggs on 'tree pods' and 'ground pods' in August and September 1995. More eggs were found on 'tree pods'.

PART II: OVIPOSITION-SITE PREFERENCES OF *N. ARIZONENSIS* AND *USCANA* SP.

AIMS

The objectives of the following experiments were to: 1) examine the oviposition-site preference of *N. arizonensis* in the field in order to comment on whether *N. arizonensis* is fulfilling its particular function, namely, targeting 'tree pods', and 2) examine the oviposition-site preference of *Uscana* sp. (*N. arizonensis* eggs on 'ground pods' or those on 'tree pods') to comment on the possible interference of *Uscana* sp. in the function of *N. arizonensis*.

METHODS

Field experiment 1

Twenty-five pods were hung in the branches of, and 25 pods were placed on the ground beneath, each of two trees at Clanwilliam (numbered C3 and C5) and two trees at Onderplaas (numbered O4 and O6). To control for the possible preference of *N. arizonensis* for a particular pod density, the 25 pods in trees and on the ground were tied in bunches of one (single pod), four, eight and twelve, with thin copper wire. Only pods picked from the trees chosen for these experiments were used. None of the pods bore *N. arizonensis* eggs before field-placement, on 30 March 1995. The pods were collected and examined a month later.

Field experiment 2

This experiment was a second attempt at detecting a preference for 'ground pods' or 'tree pods' in *N. arizonensis* oviposition, and at examining the effect of *N. arizonensis* egg location (on 'ground pods' or 'tree pods') on the rate of egg parasitism by *Uscana* sp.

At 17h00 on 01/09/1995 40 mesquite pods were offered to 60 *N. arizonensis* females in the laboratory. At 11h00 the next day, beetles were separated from pods, and the pods were sorted into two categories: those that bore fewer than five *N. arizonensis* eggs, and those that bore five or more eggs. The egg-laden pods were placed in a refrigerator to slow their development, while new pods were offered to the beetles. This procedure was repeated until, at 16h00 on 04/09/1995, 64 pods with fewer than five eggs and 61 pods with five eggs or more, had been accumulated. In this way a range of egg densities, from 1 to 19 eggs per pod, was obtained.

During the afternoon of 05/09/1995, 15 pods (eight low egg-density pods and seven high egg-density pods) were suspended in each of two trees at Clanwilliam (trees C3 and C5), and two trees at Onderplaas (trees O4 and O6). Fifteen pods were placed on the

ground beneath each of the trees, C3, C5, O4 and O6, in the same low egg-density pod / high egg-density pod ratio as that of the 'tree pods'. Within 92 hours of the start of oviposition in the laboratory, 686 *N. arizonensis* eggs had been placed in the field. The oldest eggs were 72 hours older than the youngest eggs. In physiological terms, however, the oldest eggs were probably not as well developed as normal three-day-old eggs, on account of the eggs having been refrigerated until the evening before their transfer to the field. All pods were collected and examined 17 days after field placement, on 22/09/1995.

RESULTS

Field experiment 1

Thirty days after placement in the field at Onderplaas and Clanwilliam, 3804 once-egg-free 'seeds' bore thirty-two *N. arizonensis* eggs (Table 2.1). In other words, *N. arizonensis* females oviposited on 0.8% of 'seeds' placed in the field. Only one egg was found on the pods from Clanwilliam; the rest were from Onderplaas. 'Tree pods' and 'ground pods' from tree O4 had the most eggs of all pods retrieved. Twelve of the 32 eggs found on all pods (or 38%) had been parasitized by trichogrammatids: eleven of these parasitized eggs were found on tree O4.

Chi-square analysis determined that there were significantly more *N. arizonensis* eggs on the 'tree pods' of tree O6 than on the 'ground pods' of tree O6, but that egg density was similar on the 'tree pods' and 'ground pods' of trees O4 and C5. Pods in tree C3 yielded no eggs. Similar numbers of eggs were parasitized on the 'ground pods' (six eggs) and 'tree pods' (five eggs) of tree O4. None of the 11 eggs on 'tree pods' in tree O6 was parasitized. These low numbers did not allow statistical analysis, and whether or not trichogrammatids preferentially parasitized eggs on 'ground pods' or 'tree pods', could not be resolved.

TABLE 2.1 Results of field experiment 1: Numbers (n) of parasitized (par) and unparasitized (unpar) *N. arizonensis* eggs on ground (G) and tree (T) pods hung in two trees at Clanwilliam (C3 and C5) and two trees at Onderplaas (O4 and O6). Numbers followed by the same superscript are not significantly different (Chi-square analysis, 0.05 significance level).

TREE	n PODS	n SEEDS	n EGGS (unpar)	n EGGS (par)	% par EGGS	TOTAL EGGS	% EGG-SEEDS
C3 G	25	453	0	0	-	0	-
C3 T	25	480	0	0	-	0	-
C5 G	25	436	0	0	-	0^a	-
C5 T	25	456	1	0	-	1^a	0.2
O4 G	25	515	4	6	60	10^b	1.9
O4 T	25	511	4	5	56	9^b	1.8
O6 G	25	449	1	0	-	1^a	0.2
O6 T	25	504	10	1	9	11^b	2.2
TOTAL	200	3 804	20	12	38	32	0.8

TABLE 2.2 Results of field experiment 2: The numbers (n) of eggs laid by field *N. arizonensis*, and the number of eggs parasitized by *Uscana* sp., at trees C3, C5, O4 and O6.

TREE	NUMBER OF LAB-LAID EGGS, 05/09/95	TOTAL EGGS ON RETRIEVAL, 22/09/95	NUMBER OF PARASITIZED EGGS (%), 22/09/95	NUMBER OF FIELD-LAID EGGS, 22/09/95
C3T	19	19	0	0
C3G	74	66	0	0
C5T	56	82	0	26
C5G	74	73	0	0
O4T	82	113	71 (63 %)	31
O4G	85	116	19 (16 %)	31
O6T	91	124	38 (31 %)	33
O6G	-	-	-	-
TOTAL	481	593	128 (22 %)	112

Field experiment 2

All but two of the fifteen pods suspended in tree C3 on 05/09/1995 were missing on 22/09/1995, and could not be found on the ground below that tree. Most of the pods that were hung in tree C5 had each been broken in two, presumably by wind, birds or vandals. Fortunately, all pods placed on the ground at Clanwilliam were retrieved in good condition. Goats grazed all the pods placed beneath tree O6 despite the barricade of thorny branches which successfully deterred them in the past. The pods suspended in tree O6 were in good condition upon retrieval, as were those of tree O4.

Table 2.2 contains the results of field experiment 2. No eggs were laid by field *N. arizonensis* on the 'tree pods' of tree C3, while eight eggs were lost from pods on the ground beneath that tree. On the 'tree pods' of tree C5, 26 eggs were laid by wild *N. arizonensis* females, while one egg was lost from the 'ground pods' of that tree. At the only undisturbed tree in field experiment 2, tree O4, there was no difference in the number of eggs laid by wild *N. arizonensis* females on 'tree pods' and 'ground pods'. Thirty-three eggs were laid on the 'tree pods' of tree O6 by wild *N. arizonensis* females.

No *N. arizonensis* eggs were parasitized at Clanwilliam (Table 2.2) in field experiment 2. At Onderplaas, however, 63% of the total number of eggs on tree O4 was parasitized. Only 16% of eggs on the 'ground pods' beneath tree O4 was parasitized. Thirty-one per cent of the eggs on the 'tree pods' suspended in tree O6 was parasitized upon their retrieval from the field.

Only the results from tree O4 are useful as an indication of *N. arizonensis* oviposition-site preference, and trichogrammatid oviposition-site preference, because pods in the other trees were disturbed during the course of the experiment. It appears that *N. arizonensis* oviposits with equal propensity on 'ground pods' and 'tree pods'. *Neltumius arizonensis* eggs on 'ground pods' are parasitized to a lesser extent than those on 'tree pods'. A possible reason for this is that eggs on 'ground

pod' surfaces that are in contact with the soil are less accessible to egg parasites than those on upward-facing pod surfaces.

PART III: THE RELATIONSHIP BETWEEN *N. ARIZONENSIS* EGG DENSITY AND THE DEGREE OF PARASITISM BY *USCANA* SP.

AIM

The objective of the following work was to examine the effect of variable *N. arizonensis* egg densities on the degree of parasitism by *Uscana* sp. It was necessary to know whether or not egg parasitism in the field was density dependent, and, therefore, whether or not *Uscana* sp. was capable of preventing the establishment of, or regulating the population size of, *N. arizonensis*.

METHODS

Two data sources were used to test the response of *Uscana* sp. to variation in *N. arizonensis* egg density: 1) data from the June 1994, August 1995 and September 1995 monthly pod collections, and 2) data from field experiment 2. Standard regression procedures were employed.

RESULTS

The number of parasitized eggs per pod increased linearly as the total number of eggs per pod increased (parasitoid-exploited plus unexploited pods), at Clanwilliam and Onderplaas in June 1994, and at Onderplaas in August 1995 and September 1995 (Figures 2.3 to 2.8). The proportion of parasitized eggs per pod, however, was independent of egg density per pod in five of the six analyses. In the 'ground pod' sample collected at Onderplaas in August 1995, the proportion of parasitized eggs correlated positively with egg density (Figure 2.6b). There was

FIGURES 2.3 to 2.8 Regression of a) the number of parasitized *N. arizonensis* eggs/pod against the total number of eggs/pod, and b) % parasitized eggs/pod against the total number of eggs/pod. Italicised statistics in b) refer to regression using data for exploited pods only.

FIGURE 2.3 3 June 1994: tree pods from Clanwilliam.

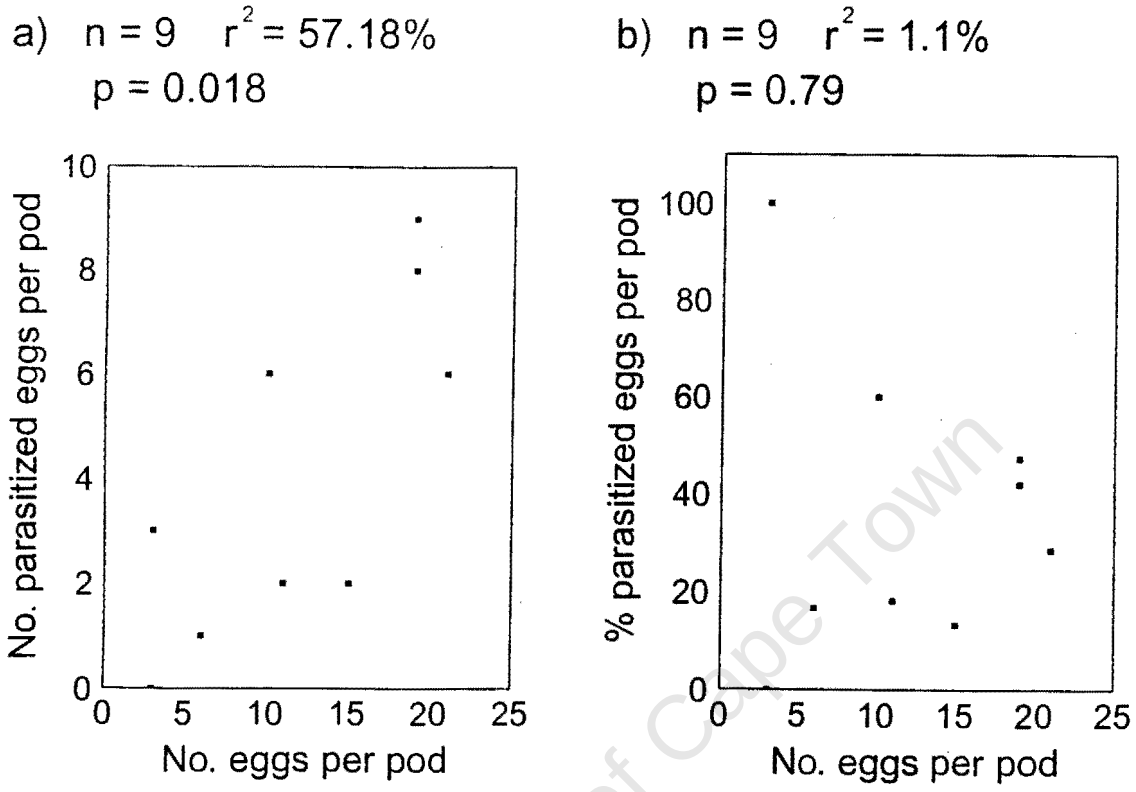


FIGURE 2.4 3 June 1994: tree pods from Onderplaas.

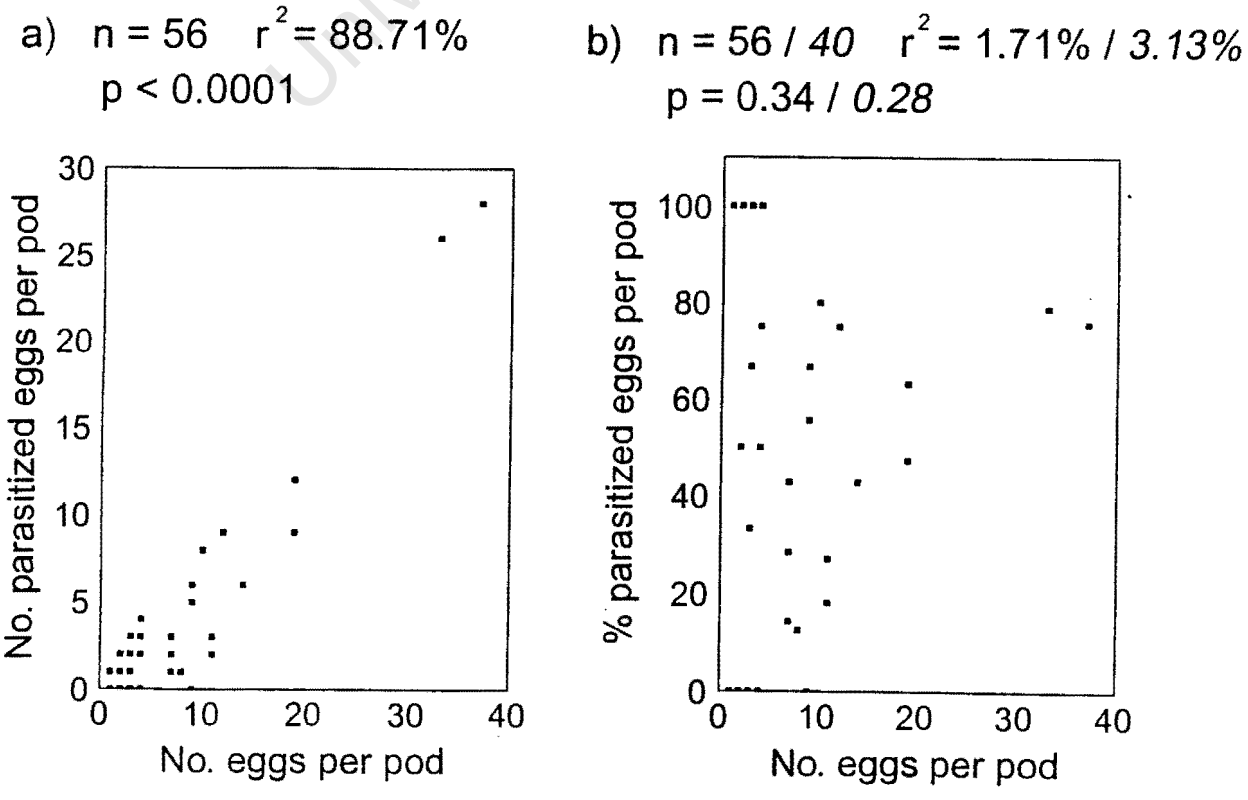


FIGURE 2.5 24 August 1995: tree pods from Onderplaas.

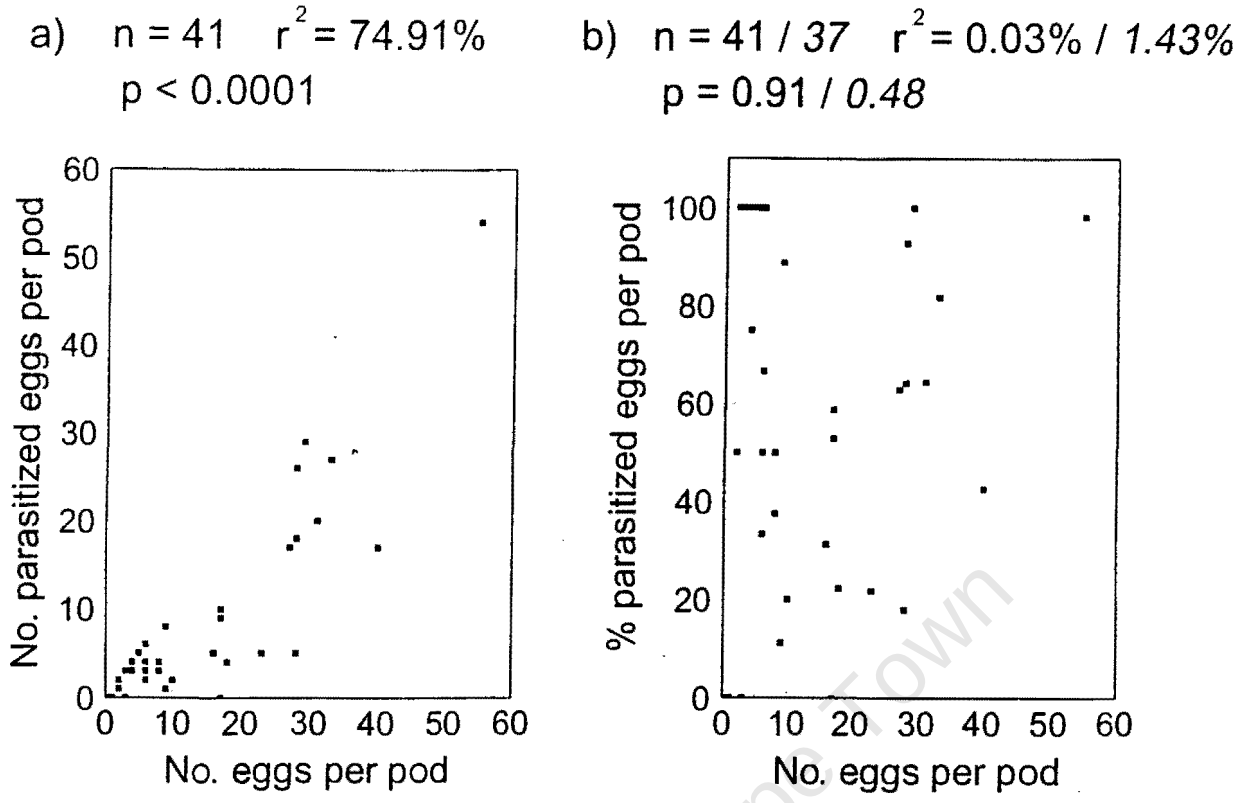


FIGURE 2.6 24 August 1995: ground pods from Onderplaas.

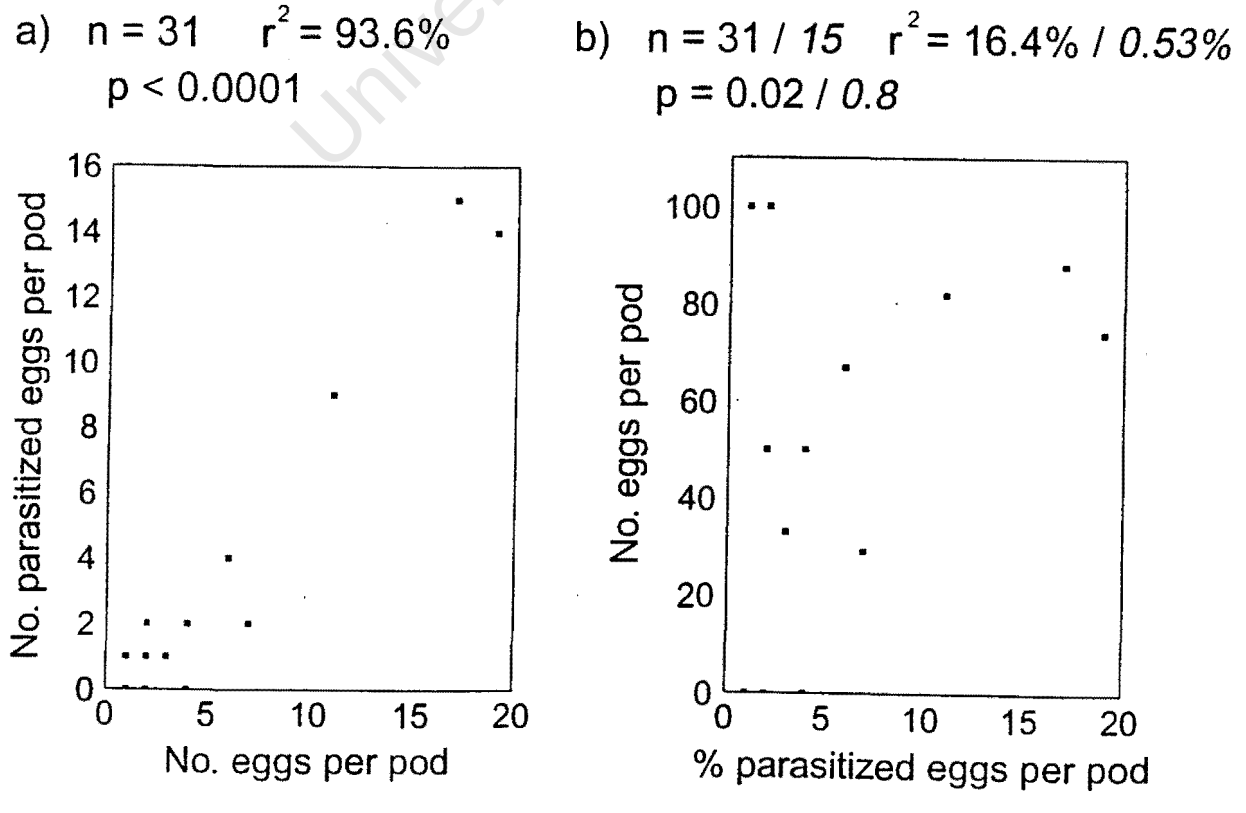


FIGURE 2.7 5 September 1995: tree pods from Onderplaas.

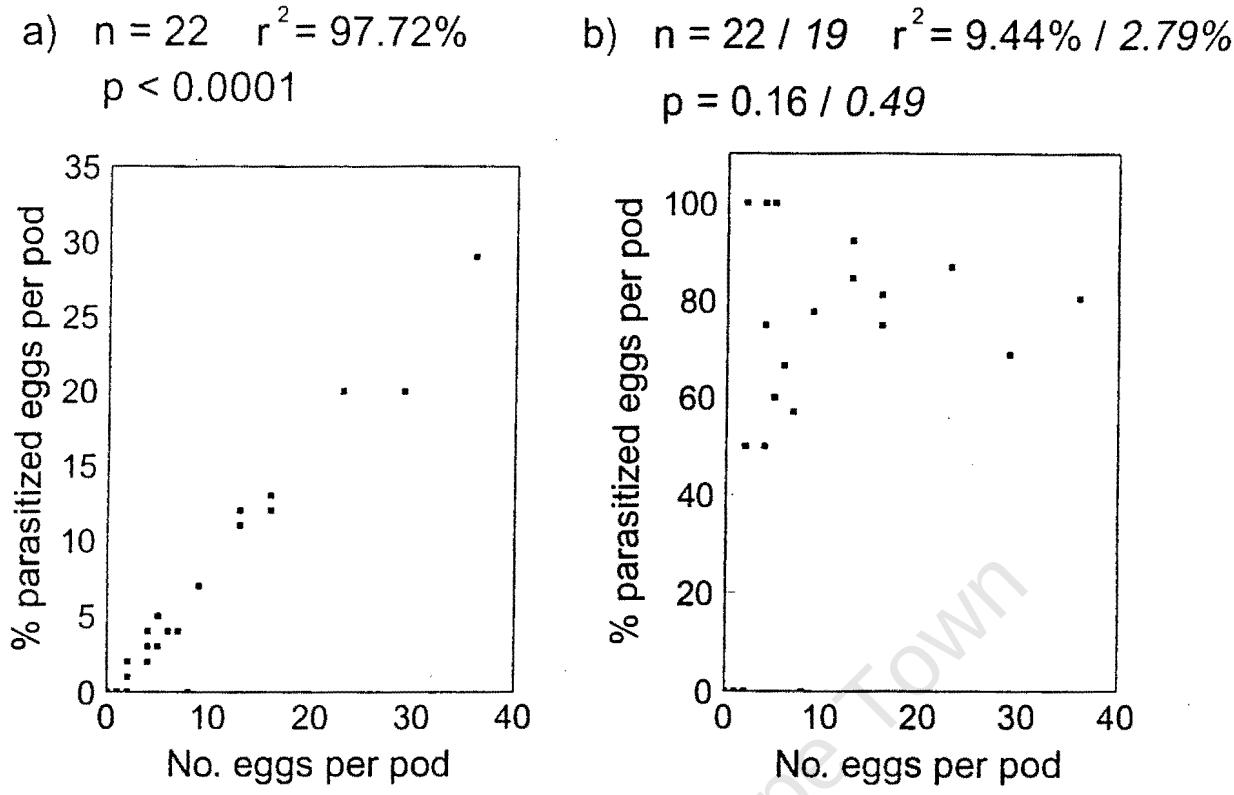


FIGURE 2.8 5 September 1995: ground pods from Onderplaas.

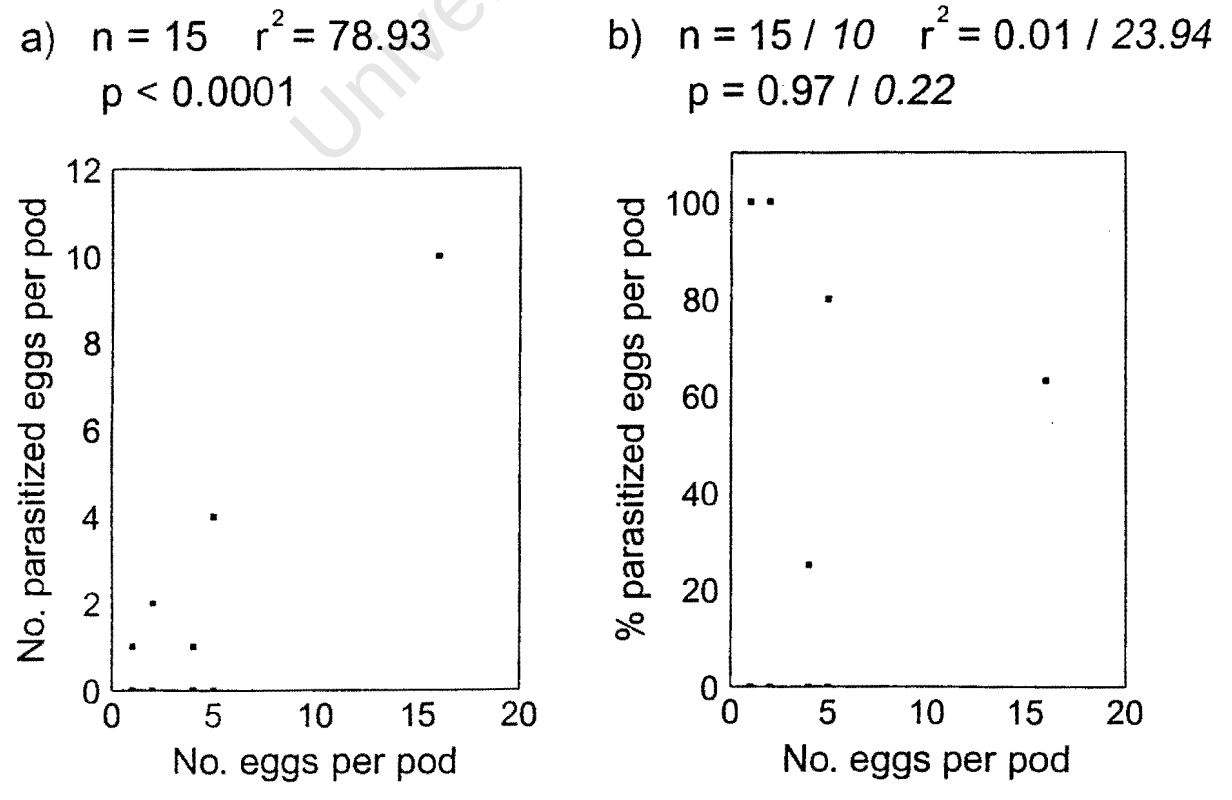


FIGURE 2.9 Ground pods from Onderplaas (tree O4): field experiment 2.

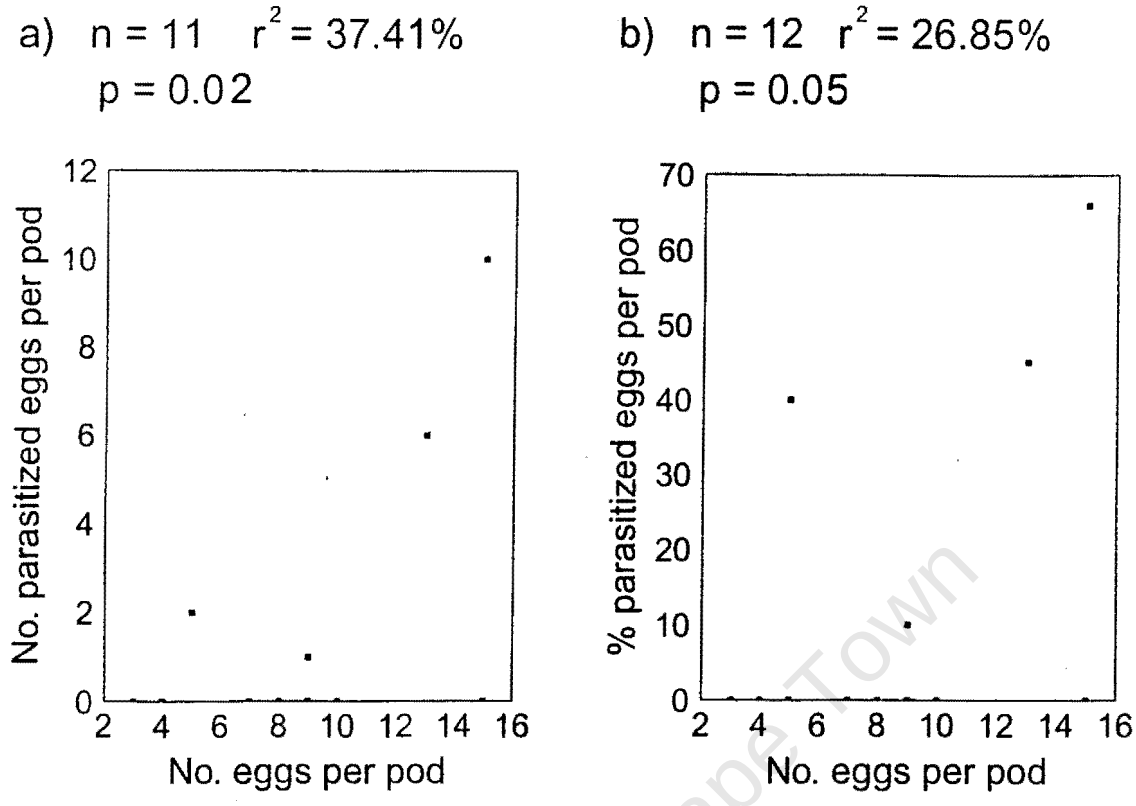


FIGURE 2.10 Tree pods from Onderplaas (tree O4): field experiment 2.

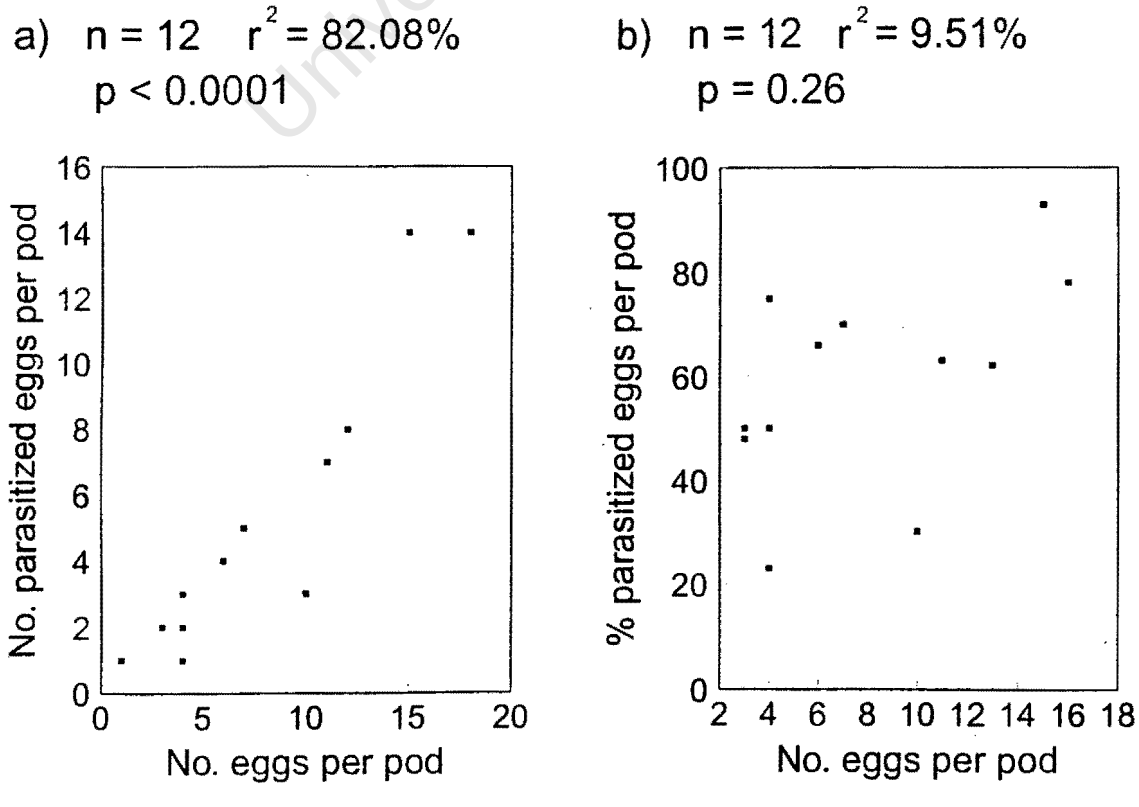


FIGURE 2.11 Tree pods from Onderplaas (tree 06): field experiment 2.

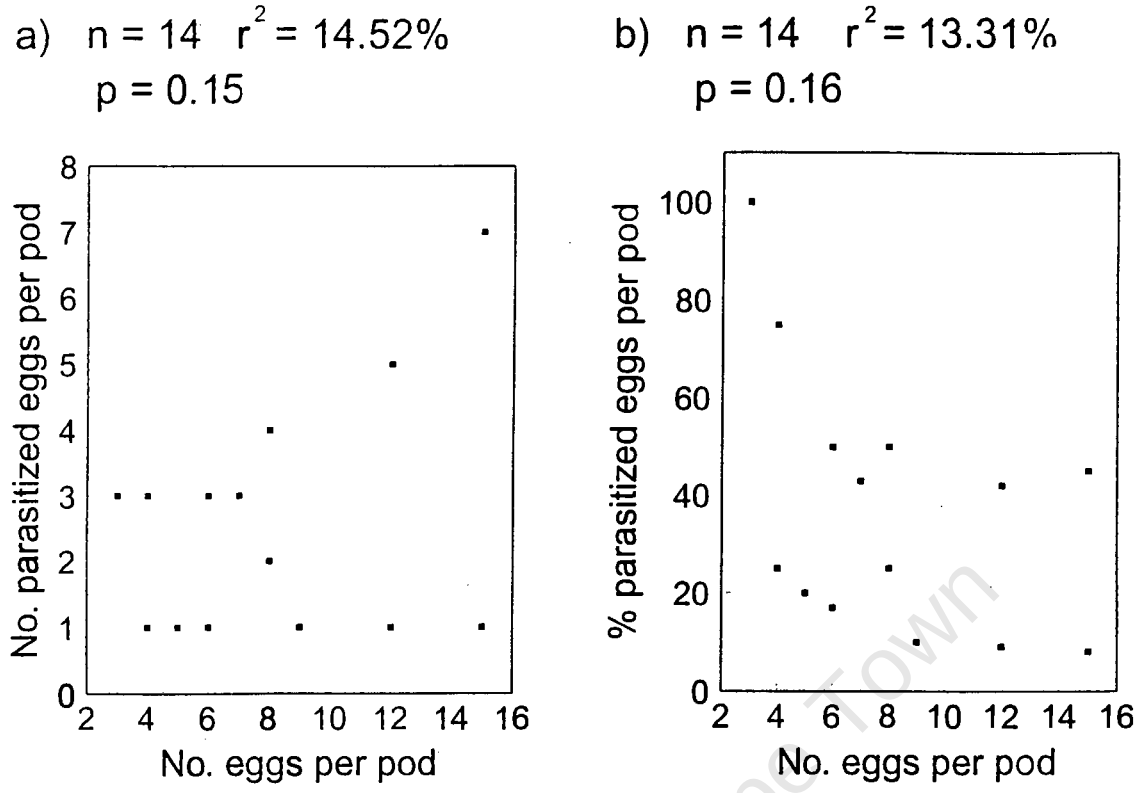
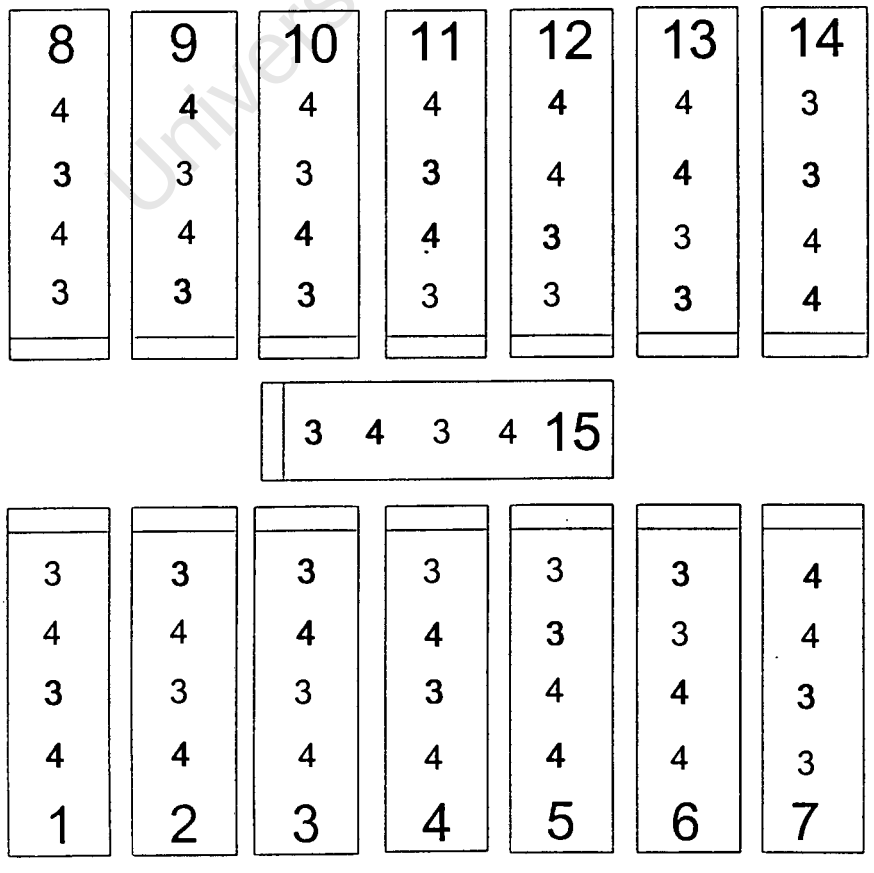


FIGURE 2.12 Arrangement of glass tubes in laboratory experiment 1. Small numbers represent the number of seeds in a segment. Bold numbers indicate fungus segments.



no correlation when only data from exploited pods were analyzed.

Data from field experiment 2 were used to explore further the density dependence of egg parasitism by *Uscana* sp. (Figures 2.9 to 2.11). The number of parasitized *N. arizonensis* eggs per pod increased linearly as the total number of eggs per pod increased, on the 'ground pods' and 'tree pods' of tree 04. The percentage parasitized eggs per pod, however, neither increased nor decreased with the total number of *N. arizonensis* eggs per pod (though it is significant, the correlation between percentage parasitized eggs per pod and total number of eggs per pod, on the 'ground pods' of tree 04, is weak). Neither the number of parasitized eggs per pod, nor the percentage parasitized eggs per pod, correlated significantly with the total number of *N. arizonensis* eggs per pod, on the 'tree pods' of tree 06 (Figure 2.11).

Data from monthly pod collections agree with those from field experiment 2: The degree of parasitism by *Uscana* sp. is independent of *N. arizonensis* egg density.

PART IV: THE PROPENSITY OF *N. ARIZONENSIS* TO OVIPOSIT ON FUNGUS-FREE PODS AND FUNGUS-COVERED PODS.

AIM

The objective of the following laboratory experiment was to determine whether or not *N. arizonensis* oviposition is affected by the presence, on pods, of fungus.

METHODS

Pods used in this experiment were collected from the same tree on 03/06/94 ('clean pods') and 09/09/94 ('fungus pods'), and had been frozen prior to use. Most 'seeds' were already bruchid-damaged when they were collected. Therefore, to obtain equivalent numbers of undamaged 'seeds' in the 'clean' and

'fungus' categories, it was necessary to use undamaged pod-segments, three 'seeds-' and four 'seeds' long. Four pod-segments were placed in each of 15 glass tubes that were stoppered with foam rubber: a three-'seeded' 'clean' segment, a four-'seeded' 'clean' segment, a three-'seeded' 'fungus' segment and a four-'seeded' 'fungus' segment. The arrangement of the tubes, and pod-segments within them, is shown in Figure 2.12.

Before the experiment began, beetles were fed a meal of pollen pellets soaked in water to optimize the production of eggs (Strathie, 1995). This was necessary to standardize the physiological conditions of beetles, so that their egg output was influenced only by the type of pod ('clean' or 'fungus'), and not by their nutritional conditions. The experiment progressed through three stages: a choice test, a starvation test and another choice test. At 16h30 on 06/10/1995, one *N. arizonensis* female was introduced into each glass tube. The first choice test lasted 49 hours. At 11h30 on 09/10/1995 all 'clean pod'-segments were removed from the tubes and the beetles were fed again. Five beetles were replaced with new individuals at this stage, because four beetles had not laid any eggs and were possibly unmated, and one beetle was lost during manipulation. The starvation test, in which only the 'fungus pod'-segments were available for oviposition, lasted 32 and a half hours. At 20h00 on 10/10/1995 another choice test began. New, 'clean pod'-segments, and the same 'fungus pod'-segments as before, were used. After 45 hours the second choice test ended.

RESULTS

Figure 2.13 displays the results of laboratory experiment 1. In the first choice test, 56 *N. arizonensis* eggs were laid on the 'clean pod'-segments by 11 beetles; 84% of these eggs were laid in the first 26 hours. No eggs were laid on the 'fungus pod'-segments in the first choice test. In the starvation test, in which only 'fungus pod'-segments were available, eight eggs were laid by three beetles, all of which were new individuals that replaced beetles lost during tube manipulation. No more *N.*

FIGURE 2.13 The number of eggs laid by all 15 *N. arizonensis* females in laboratory experiment 1.

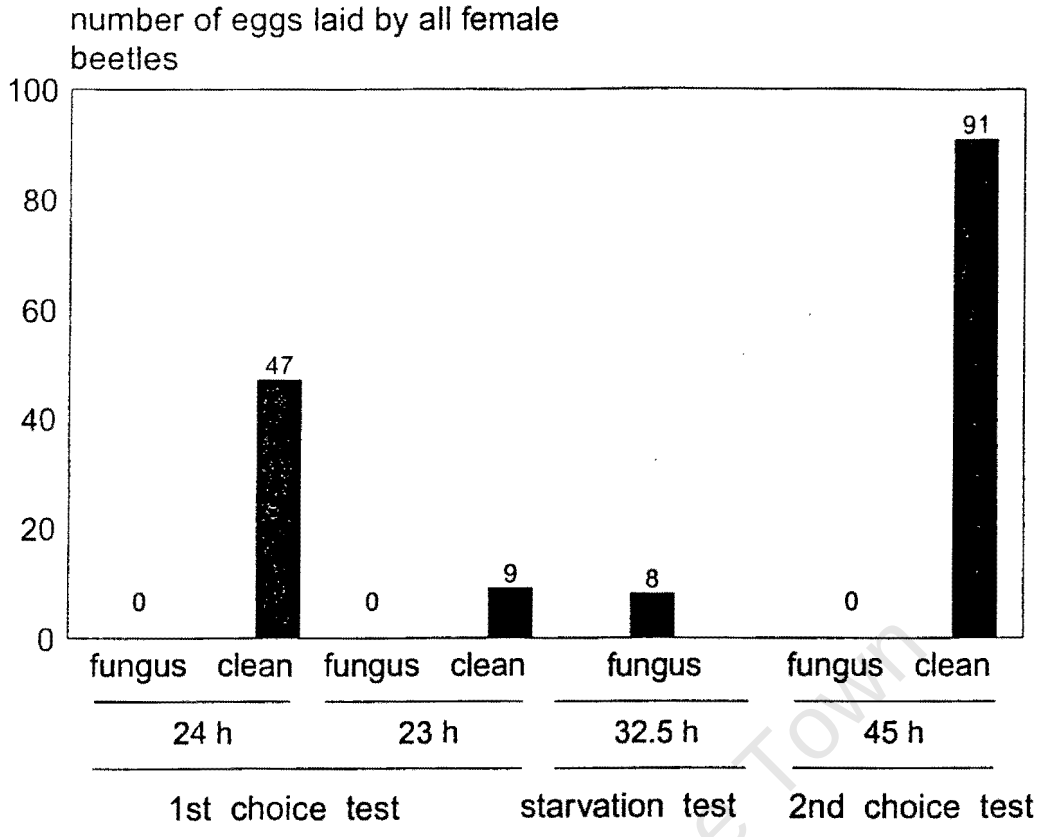
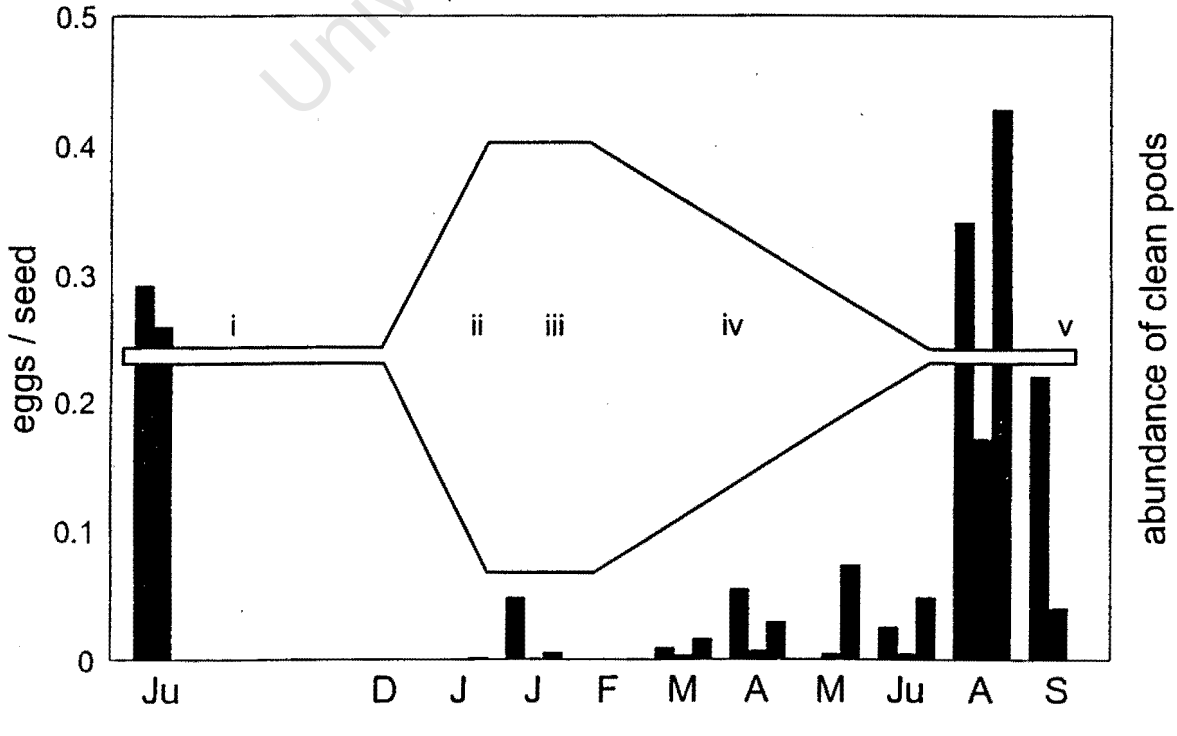


FIGURE 2.14 The seasonal variation in *N. arizonensis* egg density may be a function of the availability of clean pods.

i = All pods are on the ground. They are bruchid-damaged and fungus-covered. ii = Pods are green and immature, and tree-borne. iii = Time of peak clean-pod abundance. Pods begin to fall to the ground. iv = Pods gradually become covered with fungus. v = Very few clean pods remain at this time.



arizonensis eggs appeared on the 'fungus pod'-segments in the second choice test, but 91 eggs were laid on the new, 'clean pod'-segments. *Neltumius arizonensis* recognizes fungus-covered pods as sites for oviposition, but prefers to place its eggs on fungus-free pods when these are available.

DISCUSSION

Phenology of *N. arizonensis* oviposition

From Figure 2.2 it appears that the density of *N. arizonensis* eggs fluctuated cyclically. Relatively high egg frequencies in June 1994 were followed by a dearth of eggs in the 1995 growing season, and in August and September 1995 *N. arizonensis* eggs were common once again. On first examination of Figure 2.2 it is tempting to ascribe the observed variation in egg density to seasonal variation in *N. arizonensis* population size. This would mean that significantly larger *N. arizonensis* populations prevailed in June 1994, and in August and September 1995, than for the rest of the period sampled. But an alternative explanation for Figure 2.2 exists.

In winter, when the incidence of rain was high, pods on the water-logged ground at Clanwilliam and Piketberg became substrates for prolific fungal growth. At Piketberg this was pronounced, probably because pods were overgrown by grass and wheat, which retained moisture well. At Clanwilliam, sample trees grew on an embankment. Though there was less grass beneath these trees than at Piketberg, the relatively thick layer of pods on the ground at Clanwilliam apparently stayed wet for a long enough period to stimulate fungal growth.

'Tree pods' were often unaffected by fungus, or they were affected to a lesser extent than 'ground pods' were, probably because 'tree pods' dried quicker than 'ground pods' after downpours. Plate 2 is a photograph of pods without fungus, collected in February, and fungus-covered pods collected in September, after the winter rain. 'Tree pods' collected in

September had less fungus than 'ground pods' collected in September. No 'tree pods' were available at Piketberg in September.

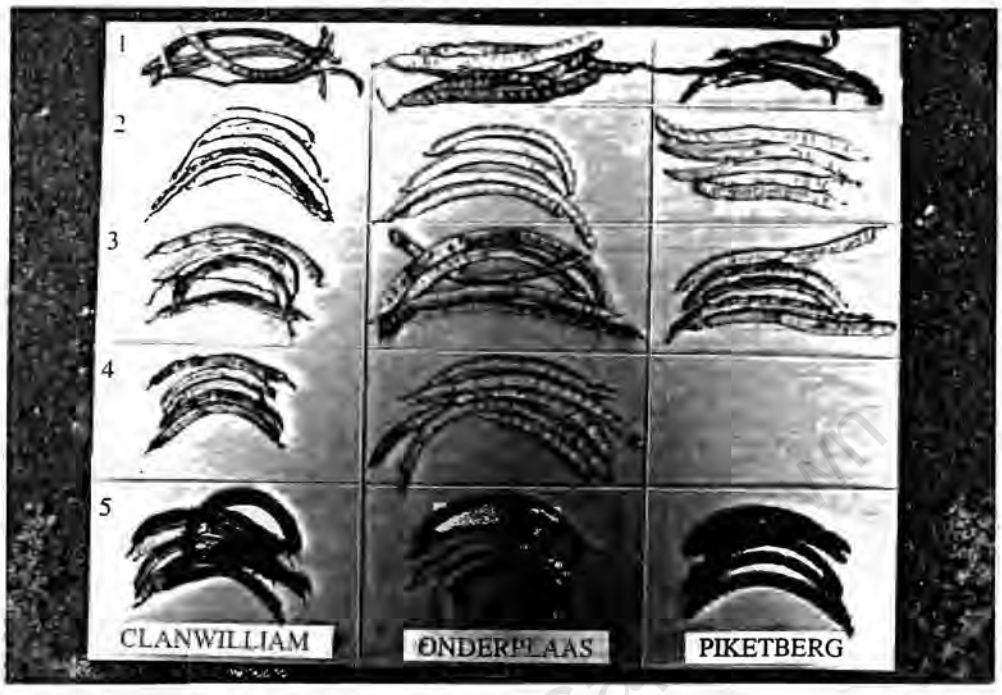


Plate 2 Fungus-infested and 'clean' pods. 1 = immature 'tree pods' collected in December 1994; 2 = 'tree pods' collected in June 1995; 3 = 'ground pods' collected in June 1995; 4 = 'tree pods' collected in September 1995; 5 = 'ground pods' collected in September 1995.

In the August and September 1995 pod collections, more eggs were found on 'tree pods' than on 'ground pods' (Figure 2.2) (the latter were extensively covered in fungus, so it could be assumed that they had been on the ground for a considerable period). The eggs on 'tree pods' therefore contributed more to the high egg density recorded in Figure 2.2, than did the eggs on 'ground pods'. *Neltumius arizonensis* prefers to oviposit on pods that do not harbour fungus. After the winter rain, therefore, there effectively remained fewer 'seeds' that were suitable for *N. arizonensis* oviposition (the few pods that hung in trees) than the number that was available in summer, before pods became fungus-infested. With only 'tree pods' available as oviposition sites, *N. arizonensis* eggs became concentrated on them. The

observation that single 'seeds' on some 'tree pods' held up to 10 eggs, attests to unusually high egg densities on these pods. Evidence from laboratory tests supports the contention that 10 eggs per 'seed' is an unusually high egg density: Strathie (1995) reported that *N. arizonensis* females preferred to oviposit on 'seeds' which were not already occupied by a conspecific egg.

Neltumius arizonensis has been shown to oviposit fewer eggs on pods that have been previously damaged by bruchids, and which are studded with their exit holes (Strathie, 1995). In this study, exit holes may therefore have acted, as fungus did, to deter *N. arizonensis* oviposition, and to cause *N. arizonensis* eggs to be concentrated on 'tree pods'. Chapter 3 presents evidence that *A. prosopis*, which emerged in far greater numbers than *N. arizonensis* did, prefers to utilize 'ground pods'.

It is therefore possible that *N. arizonensis* population sizes did not grow and diminish, but that a small, constant *N. arizonensis* population prevailed: The seasonal variation in egg density was possibly a function of the availability of 'clean' pods. This concept is illustrated in Figure 2.14. The model proposed above is partly based on circumstantial evidence. It serves to provide an alternative explanation for the observed variation in field *N. arizonensis* egg density, rather than the final word.

Preference of *N. arizonensis* for 'tree pods' or 'ground pods', and preference of *Uscana* sp. for eggs on 'tree pods' or 'ground pods'.

Field experiments 1 and 2 did not yield satisfactory results. Factors which may have caused their failure included ant predation (which was not examined specifically in this study), and vandalism. It is difficult to conclude whether *N. arizonensis* prefers to oviposit on 'tree pods' or 'ground pods', and whether or not *Uscana* sp. preferentially parasitizes *N. arizonensis* eggs on 'tree pods' or 'ground pods' remains unresolved.

In north-western Costa Rica, an average of 50% of unhatched bruchid eggs was removed from the pods of *Acacia farnesiana* (L.) by ants (Traveset, 1990). Hoffmann (1982) showed that the predation of eggs by ants was an important factor preventing the establishment of *Tucumania tapiacola* Dyar (Lepidoptera: Phycitidae) on *Opuntia aurantiaca* Lindley in South Africa. Robertson (1985) drew a similar conclusion for *Cactoblastis cactorum* (Berg), a biological control agent of *O. ficus-indica* (L.) Miller and *O. aurantiaca* in South Africa.

Evidence that *N. arizonensis* prefers to oviposit on 'tree pods' comes from two sources:

1) In August and September 1995, more eggs were found on 'tree pods' than on 'ground pods'. Whether or not *N. arizonensis* preferred the spatial position of 'tree pods' to that of 'ground pods', however, cannot be commented on by this observation. Probably the degree of fungal infection of pods influenced female beetles' decisions regarding the placement of their eggs.

2) In field experiment 2, 26 eggs were laid on the 'tree pods' hung in tree C5, but the 'ground pods' placed beneath that tree lost 1 egg. That this reflects a true preference for 'tree pods' is less likely since wild *N. arizonensis* females possibly laid more eggs on the 'tree pods' for the reason that some laboratory-laid eggs were removed from these pods in the field. In other words, wild *N. arizonensis* females may have been less deterred by conspecific eggs on the 'tree pods', because there were fewer eggs on them, than they were by those on the 'ground pods' beneath that tree.

Similarly, the test for a preference of *Uscana* sp. for eggs on 'tree pods' or 'ground pods' did not yield conclusive results. In field experiment 2, results from tree O4 suggest that *N. arizonensis* eggs on 'ground pods' are not parasitized as often as those on 'tree pods'. This could, however, be attributed to the fact that eggs on the surface of a pod that is in contact with the soil, are physically out of the reach of egg parasitoids. A true preference for eggs on 'tree pods' could

only be deduced from an experiment in which all eggs on 'ground pods' are adequately exposed to parasitoids, as those on 'tree pods' probably are, and in which the degree of egg parasitism on 'ground pods' is still lower.

Newton (1988) reported that in one citrus orchard out of three, parasitism of *Cryptophlebia leucotreta* (Meyrick) (Tortricidae) by *Trichogrammatoidea cryptophlebiae* Nagaraja (Trichogrammatidae) was higher at the tops of orange trees than at the tree bottoms (1.5m and 0.5m above the ground, respectively). Overall, however, rates of egg parasitism at the tops and bottoms of orange trees were not significantly different.

The general issue of interference by native parasitoids with weed biocontrol agents is discussed in Chapter 3.

The effect of *N. arizonensis* egg density on the degree of trichogrammatid parasitism.

In the analysis of egg parasitism by *Uscana* sp., a single mesquite pod was regarded as a patch (*sensu* Hassell, 1982) of unparasitized and parasitized eggs. Though bruchids lay single eggs rather than clumps of eggs, as Lepidoptera do, this concept was appropriate because pods ("patches of eggs") were spatially isolated from one another.

Four types of responses by insect parasitoids to spatial variation in host density are recognized (Lessels, 1985; Ehler *et al.*, 1987): direct density dependent, inverse density dependent, density independent and "dome" shaped. It was previously believed that insect population stability would be enhanced by density dependent host mortality, and reduced if mortality was inversely density dependent (Hassell, 1982). It is now known that inverse density dependent host mortality may also be stabilizing (Hassell, 1984, cited by Ehler *et al.*, 1987). Murdoch *et al.* (1985) reported that density dependent responses are uncommon in nature, and that inverse density dependent and

density independent patterns are more often recorded.

In this study, parasitism of *N. arizonensis* eggs by *Uscana* sp. was density dependent in only two instances out of nine. The correlations between percentage parasitized eggs per pod and the total number of eggs per pod in these instances, however, were weak. In the other seven instances in which egg parasitism data were subjected to regression analysis, percentage egg parasitism was independent of egg density.

Ehler *et al.* (1987) drew attention to the distinction between egg patches that are exploited by parasitoids, and those that are unexploited, in the analysis of patch exploitation dynamics of egg parasitoids. They purported that it is important to analyze egg parasitism data separately; those relating to exploited patches only, and those from exploited and unexploited patches combined. Ehler *et al.* (1987) implied that density dependent relationships between egg availability and the degree of parasitism, may be obscured by the inclusion of unexploited egg patches, though their results did not support this contention. In this study a density dependent relationship became density independent when unexploited egg patches were ignored, in one case out of two. In the other case the sample was too small to do separate analyses.

Some reasons for the functional response of a parasitoid being more density independent than density dependent, have been studied. The "handling time", or the time between encountering a host and the resumption of host search, may limit the maximum attack rate per parasitoid at high host densities (Holling, 1959, cited by Varley *et al.*, 1975). Another possibility is that parasitoids suffer egg limitation at high host densities (Varley *et al.*, 1975). Interference between searching parasitoids, when more than one parasitoid is present, is known to affect searching efficiency negatively in some species. Furthermore, the degree of interference is thought to increase with increasing parasitoid density (Varley *et al.*, 1975).

Although *Uscana* sp. was sometimes able to parasitize large numbers of *N. arizonensis* eggs, it generally did not respond to variation in the density of *N. arizonensis* eggs in a directly dependent or inversely dependent manner. For this reason, *Uscana* sp. will probably not be an important factor in preventing the successful establishment of *N. arizonensis*. Detailed life-table analysis of successive *N. arizonensis* generations would have to be conducted over several seasons to verify this. Such an analysis was beyond the scope of the present study.

CHAPTER 3: SEASONAL BRUCHID EMERGENCE, THE INCIDENCE OF LARVAL AND PUPAL PARASITISM, AND THE DEGREE OF MESQUITE SEED DAMAGE

SUMMARY

The emergence of *A. prosopis*, *N. arizonensis* and parasitic Hymenoptera from mesquite pods was monitored at Clanwilliam, Onderplaas and Piketberg in 1994 and 1995. *Neltumius arizonensis* was recorded at much lower densities than *A. prosopis*, and *N. arizonensis* began to emerge later in the year than *A. prosopis*. *Algarobius prosopis* utilized tree-borne, green pods with poorly developed cotyledons in December 1994, but no *N. arizonensis* individuals were collected from these pods.

The percentage parasitism of *A. prosopis* and *N. arizonensis* larvae and pupae was 0.83% over a period of twelve months. Eupelmidae, Pteromalidae, Eulophidae and Torymidae were reared from mesquite pods.

In 1994 the level of seed damage increased with time, until 56% of seeds and 69% of seeds were destroyed in November, at Piketberg and Clanwilliam, respectively. Usually, fewer seeds were damaged in 'tree pods' than in 'ground pods'. Fewer seeds were damaged in 1995 than in the previous year.

AIMS

With the work reported in this chapter, answers to the following questions were sought:

1) Does *N. arizonensis* continue to emerge from mesquite pods, and how abundant is this species compared to *A. prosopis*?

2) Does the emergence of *N. arizonensis* indicate a preference for 'tree pods' in this species?

3) To what degree are larvae and pupae of the introduced bruchids parasitized by native Hymenoptera?

4) What percentage of mesquite seeds is destroyed by the introduced bruchids?

METHODS

Bruchid and parasitoid emergence

The dates on which pod collections took place and the numbers of trees sampled, are listed in Table 3.1. Table 3.2 contains the numbers of seeds sampled and the numbers of adult bruchids reared from them. Monitoring of insect emergence from pods collected in the field began in June 1994, and ended in September 1995. From June until December 1994, only 'ground pods' were collected. Because goats unexpectedly grazed most of the pods at Onderplaas in July 1994, data collection could only resume there when the new seed crop appeared in December 1994. In January 1995 fences were erected around sample trees at Onderplaas. Monitoring of the 1995 seed crop, which began in December 1994 and ended in September 1995, involved the collection of both 'tree pods' and 'ground pods'. Five trees were marked at each site, which was visited once every 30 to 40 days for pod collection.

TABLE 3.1 The number of trees sampled for ground (G) and tree (T) pods at each site and collection date. FACI = F.A.C. Impson, WC = W. Coetzer, JHH = J.H. Hoffmann. Dates in bold print are those at which pods were checked for *N. arizonensis* eggs.

DATE	COLLECTOR	CLANWILLIAM		ONDERPLAAS		PIKETBERG	
20/01/94	FACI	NONE		G=6	T=0	NONE	
08/03/94	FACI	G=3	T=0	G=6	T=0	G=2	T=0
29/04/94	FACI	G=3	T=0	G=9	T=0	G=4	T=0
03/06/94	WC	G=6	T=1	G=9	T=3	G=6	T=0
11/07/94	WC	G=5	T=0	NONE		G=5	T=0
09/08/94	WC	G=5	T=0	NONE		G=5	T=0
09/09/94	WC	G=5	T=0	NONE		G=5	T=0
12/10/94	WC	G=5	T=0	NONE		G=5	T=0
20/11/94	WC	G=5	T=0	NONE		G=5	T=0
01/12/94	WC	G=0	T=5	G=0	T=5	G=0	T=5
04/01/95	WC	G=0	T=5	G=0	T=5	G=0	T=5
18/01/95	WC	G=0	T=5	G=5	T=5	G=4	T=5
23/02/95	WC	G=5	T=5	G=5	T=2	G=5	T=4
30/03/95	WC	G=5	T=5	G=5	T=2	G=5	T=5
29/04/95	WC	G=5	T=2	G=5	T=1	G=5	T=2
30/05/95	WC	G=5	T=3	NONE		G=5	T=1
29/06/95	WC	G=5	T=3	G=2	T=2	G=5	T=1
24/08/95	JHH	G=1	T=1	G=3	T=3	G=1	T=1
05/09/95	WC	G=5	T=2	G=1	T=2	G=5	T=0
TOTAL		G=68	T=37	G=66	T=30	G=72	T=29

TABLE 3.2 The number of seeds (undamaged plus damaged) **(a)**, *A. prosopis* individuals **(b)** and *N. arizonensis* individuals **(c)** collected at Clanwilliam, Onderplaas and Piketberg from 03/06/1994 until 05/09/1995. Figures marked with asterisks are data from tree pods.

DATE	CLANWILLIAM			ONDERPLAAS			PIKETBERG		
	a	b	c	a	b	c	a	b	c
03/06/94	18 897	1021	76	28 933	508	9	17 155	1478	128
11/07/94	13 538	796	72	-			9 049	850	69
09/08/94	8 232	188	22	-			9 166	750	21
09/09/94	8 632	112	9	-			8 709	316	8
12/10/94	5 903	41	0	-			4 996	175	6
20/11/94	3 946	59	3	-			4 449	88	6
01/12/94	* 2 279	8	0	* 2 083	30	0	* 1 861	1	0
04/01/95	* 6 043	164	0	* 3 846	37	0	* 1 934	75	0
18/01/95	*11 395	248	1	* 5 155	120	0	* 3 590	125	0
	9 291	323	27				4 721	147	0
23/02/95	*10 114	133	3	* 3 524	35	2	* 4 321	37	0
	12 069	793	5	11 778	241	3	7 955	158	1
30/03/95	* 3 219	62	0	* 780	1	0	* 3 150	88	22
	8 694	874	6	8 574	310	28	8 137	541	16
29/04/95	* 1 166	5	1	* 595	2	0	* 1 280	9	7
	10 654	465	10	7 556	284	20	13 149	527	20
30/05/95	* 4 196	0	1	-			* 954	4	4
	6 918	72	2	-			5 621	133	10
29/06/95	* 1 026	0	0	* 1 556	1	0	-		
	4 684	95	3	4 022	326	33	-		
24/08/95	* 1 653	2	11	* 743	9	14	* 225	3	5
	2 495	141	17	2 730	52	8	33	11	5
05/09/95	* 1 868	6	0	* 931	16	6	-		
	6 813	110	3	2 283	180	8	5 761	66	2
TOTAL	*42 959	628	17	*19 213	251	22	*17 315	342	38
	111 475	4531	228	75 167	2224	136	98 901	5240	292

Approximately 500g of mesquite pods were collected from each sample tree. The pods were placed in 16cm X 36cm transparent, plastic boxes. A piece of tulle, held in place by the lid's rim, covered the box. The centre of the lid was cut out to allow air flow.

Sample boxes were returned to an insectary in which the temperature averaged 26.5°C, and in which relative humidity was 58%. The light was left on for 24h a day. In order to prevent insectary-reared, adult insects from ovipositing on seeds containing larvae originating from the field, *A. prosopis* and *N. arizonensis* adults were removed from sample boxes every three days. Pods from each sampling occasion were kept for about 30 days. When insects were collected from sample boxes, an ultraviolet light attracted them onto the sides of a tulle cage, from which they were collected in glass vials and frozen overnight. The numbers of *A. prosopis*, *N. arizonensis* and parasitoid wasps emerging from each sample box were thus recorded every 30 to 40 days. For the calculation of beetle emergence rate per seed (b/s), the total number of beetles that emerged in 30 days from all trees sampled at a site on a particular date (b_{30}), was divided by the total number of seeds in the 500g samples from which the beetles emerged (s_t) minus the number of seeds destroyed at that site the previous month (s_d) (equation 1).

equation 1:
$$b/s = \frac{b_{30}}{(s_t - s_d)}$$

The total number of seeds in a single-tree sample was obtained by the proportional relationship between whole sample mass and the mass of a sub-sample of twenty-five pods. Pods were weighed using a Mettler PM 460 electronic balance.

Beetle emergence data (expressed as beetles per seed) were log-transformed, because the frequency of *N. arizonensis* emergence was, on average, an order of magnitude lower than that of *A. prosopis*.

Seed damage

After 30 days all pods were frozen overnight. Seed damage was estimated by counting, in the same randomly chosen twenty-five-pod sub-sample, the total number of seeds and the number of beetle emergence holes. One emergence hole represented one seed damaged by a single bruchid beetle. The number of seeds destroyed by bruchids was expressed as a percentage of the total number of seeds in 25 pods.

RESULTS

Bruchid emergence

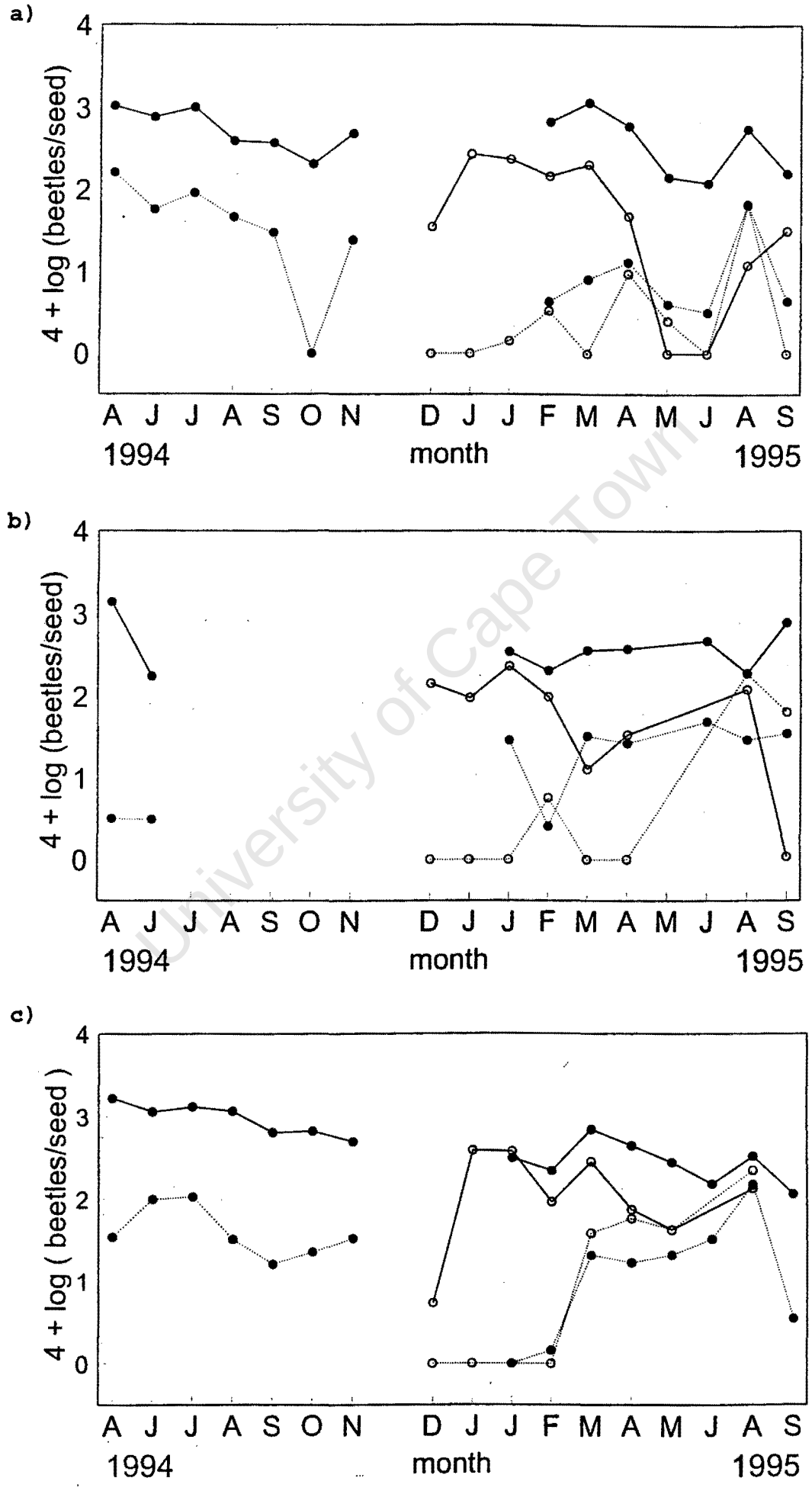
Clanwilliam

At Clanwilliam, the overall rates of *A. prosopis* and *N. arizonensis* emergence decreased from April until November in 1994 (Figure 3.1a). During this period *A. prosopis* was much more abundant than *N. arizonensis*. Minor increases in emergence of both bruchid species occurred in July 1994.

From December 1994 until April 1995, more *A. prosopis* emerged from 'tree pods' than *N. arizonensis* (Figure 3.1a). No *N. arizonensis* emerged from green pods with poorly-developed cotyledons, collected in December 1994. Only *A. prosopis* was collected from the mature pods with developed cotyledons collected in early January 1995.

In May 1995 both bruchid species were less abundant in 'tree pods' and 'ground pods' than in the preceding months, and the dearth of beetles persisted until August. 'Ground pods' were preferred over 'tree pods' by *A. prosopis* in 1995. Overall, far fewer *N. arizonensis* emerged than *A. prosopis* in 1995, and *N. arizonensis* individuals were almost equally abundant in samples of 'ground pods' and 'tree pods', in contrast to *A. prosopis*. In September 1995 the emergence of *N. arizonensis*, and that of *A. prosopis* from 'ground pods', decreased, but *A. prosopis* was

FIGURE 3.1 Seasonal emergence of *N. arizonensis* (broken lines) and *A. prosopis* (solid lines), from ground pods (closed circles) and tree pods (open circles). a) Clanwilliam, b) Onderplaas, c) Piketberg.



more common in 'tree pods' in September 1995 (Figure 3.1a).

Onderplaas

Few pods were collected at Onderplaas in 1994 because of interference by goats. In 1995, *A. prosopis* was more abundant than *N. arizonensis* at Onderplaas (Figure 3.1b). Only *A. prosopis* was collected from immature 'tree pods' in December 1994 (see plate 2), and from mature 'tree pods' in early January 1995. Both bruchid species emerged from 'ground pods' more often than from 'tree pods', for most of the sampling period in 1995. A notable exception to this was the high emergence rate of both bruchid species from 'tree pods' in August compared to April 1995 (Figure 3.1b).

Piketberg

In 1994, *N. arizonensis* emergence at Piketberg fluctuated more than that of *A. prosopis*, and *N. arizonensis* was far less abundant than *A. prosopis* (Figure 3.1c). Lower numbers of *Algarobius prosopis* were reared toward the end of 1994, in comparison with the earlier part of the year.

In 1995 *A. prosopis* was encountered more often in samples of 'ground pods' than in 'tree pod' samples, for most of the sampling period. *Neltumius arizonensis* individuals were not reared from immature 'tree pods' collected in December 1994, nor were they obtained from samples of mature 'tree pods' in early January. *Neltumius arizonensis* emergence was, however, more frequent in 'tree pod' samples than in 'ground pod' samples, after February. Emergence of both bruchid species from 'tree pods' and 'ground pods' increased in March 1995, possibly because of high temperatures in February (South African Weather Bureau, Pretoria).

Algarobius prosopis emergence from 'ground pods' decreased from March until June 1995, and from March until May 1995 progressively fewer beetles of this species were reared from 'tree pods'. Both bruchid species were more abundant in 'ground

pods' in August than in June, and 'tree pods' yielded more bruchids in August than in May 1995 (Figure 3.1c).

Parasitism of bruchid larvae and pupae

Over a period of twelve months, from June 1994 until the following June, 98 chalcidoid wasps (excluding Eulophidae) were collected from pod samples (Table 3.3 and associated collection of chalcidoid wasps). These were presumed to be solitary endo- or ectoparasites of the larvae and pupae of *A. prosopis* and *N. arizonensis*. That at least one indigenous chalcidoid wasp species (*Entedon* sp.) has adopted *N. arizonensis* as a host, was confirmed by the emergence of a wasp of this species from a mesquite seed which bore a hatched *N. arizonensis* egg.

TABLE 3.3 Identities and accession numbers of wasps in the accompanying collection were obtained by comparison with the wasps of Hoffmann *et al.* (1993). The wasps of these authors were identified by the staff of the Biosystematics Division of the Plant Protection Research Institute, Agricultural Research Council, Pretoria. Those species without accession numbers were not collected by Hoffmann *et al.* (1993).

EULOPHIDAE		
ACUCT 349	.....	*Entedon* sp.
EUPELMIDAE		
ACUCT 333	.....	Undetermined species
ACUCT 346	.....	*Eupelmus ?urozonus* Dalman
ACUCT 347	.....	*Eupelmus* sp.
-	.....	Undetermined species
PTEROMALIDAE		
ACUCT 332	.....	*Dinarmus actifrons* (Walker)
TORYMIDAE		
-	.....	Undetermined species
TRICHOGRAMMATIDAE		
-	.....	*Uscana* sp.

For the purpose of identification, all wasps were compared to wasps collected from mesquite pods by Hoffmann *et al.* (1993a). Fifty-nine wasps were eupelmids, 29 were pteromalids and 10 were torymids. In addition, about 250 eulophids were collected. Twenty-five of these eulophids were found in a single, dissected mesquite seed, so this species was presumed to be gregarious, polyembryonic or superparasitic.

In the same twelve-month period, 12 434 *A. prosopis* individuals and 618 *N. arizonensis* individuals were reared from the same pod samples as those from which the chalcidoid wasps were obtained. It was assumed that each eupelmid and pteromalid, and each separately collected group of eulophids, parasitized either an *A. prosopis* or *N. arizonensis* larva or pupa, and not the immature stages of an indigenous bruchid species, or some other, incidentally collected indigenous insect. The overall rate of parasitism of *A. prosopis* and *N. arizonensis* larvae and pupae was 0.83%. The torymid wasps were not included in this calculation because they were probably seed endophages (Prinsloo, 1985).

Seed damage

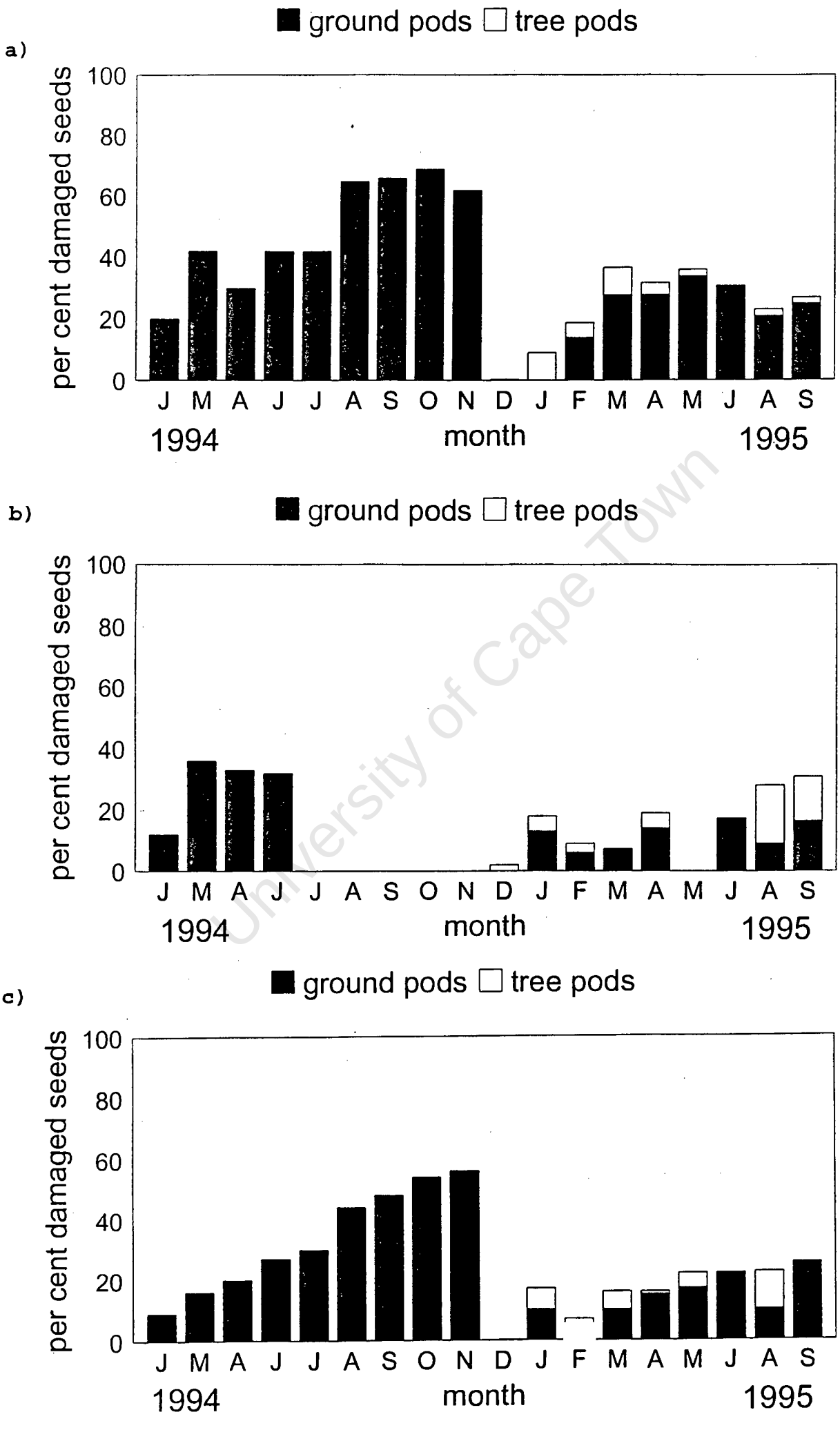
Clanwilliam

The percentage of damaged seeds in 'ground pods' at Clanwilliam increased from 20% in January 1994 to 69% in October 1994 (Figure 3.2a). Far fewer seeds were damaged in 1995 in comparison to the previous year. In September 1995 only 25% damage was recorded in 'ground pod' samples, but 65% of seeds were bruchid-damaged in the same month in 1994. In all pod samples collected at Clanwilliam in 1995, 'ground pods' were damaged more extensively than 'tree pods'.

Onderplaas

At Onderplaas, 38% of seeds in a sample of 'ground pods' were bruchid-damaged in March 1994 (Figure 3.2b). From January until April 1995, 'ground pods' were damaged more extensively

FIGURE 3.2 Monthly levels of seed damage at Clanwilliam (a), Onderplaas (b) and Piketberg (c).



than 'tree pods'. In August 1995, however, more seeds were damaged in 'tree pods' than in 'ground pods' (19% and 9% respectively), and in September only marginally more seeds in 'ground pods' were damaged by bruchids than in 'tree pods'. In 1995 the levels of seed damage in 'ground pod' samples at Onderplaas were still low in August and September.

Piketberg

The number of seeds damaged in 'ground pods' at Piketberg increased steadily from 10% in January 1994 to 56% in November 1994 (Figure 3.2c). In September 1995 fewer (26%) seeds were damaged in 'ground pod' samples, than in September 1994 (48%). In August 1995, similar numbers of seeds in 'tree pods' and 'ground pods' were damaged (12% and 10% respectively), but usually the degree of seed damage in 'ground pod' samples was higher than that in samples of 'tree pods'.

DISCUSSION

The following general trends in bruchid emergence were detected:

1) At all sites in 1994 and 1995, *A. prosopis* was much more common than *N. arizonensis*;
2) *Algarobius prosopis* and *N. arizonensis* emergence tended to decrease toward the end of 1994 at Clanwilliam and Piketberg;
3) Green, immature 'tree pods' were used by *A. prosopis*, but not by *N. arizonensis*;
4) *Algarobius prosopis* was more abundant than *N. arizonensis* in 'tree pods' in the early part of 1995, but emergence of the former species from 'tree pods' tended to decline from February until May;
5) Usually, more individuals of both bruchid species emerged from 'ground pods' than from 'tree pods';
6) Numbers of emerging adult bruchids increased in March 1995 and August 1995.

Bruchid emergence in relation to abiotic factors

The rise in bruchid numbers in March 1995 was probably due to the increased rate of development of bruchid larvae, initiated by high summer temperatures. Ahmed *et al.* (1995) reported that emergence of adult bruchids from pods of *Albizia* spp. in India was positively correlated with temperature, but that rainfall affected bruchid emergence negatively. Kistler (1985) stated that the developmental rates of both *A. prosopis* and *N. arizonensis* increased with increasing laboratory temperature, but he did not test the relationship between ambient temperature and the numbers of adult bruchids that emerged in the field. Kistler (1985) did examine the effect of rainfall on bruchid emergence, and concluded that the number of adult bruchids emerging from mesquite pods was positively correlated with this environmental variable.

The differing success rates of *A. prosopis* and *N. arizonensis*

The most important conclusion to be drawn from the examination of Figures 3.1a, b and c, is that *N. arizonensis* was present in mesquite pods at all three sites, for most of this study's sixteen month duration. It is encouraging that *N. arizonensis* emergence increased to its highest recorded level in August 1995, in 'ground pods' and 'tree pods' at Clanwilliam and Piketberg. Just as the high densities of *N. arizonensis* eggs on fungus-free 'tree pods' in June 1994, and in August and September 1995 may have been misleading, however, this increase in *N. arizonensis* emergence may be a sampling artefact. If the 'ground pods' from which these beetles emerged were still fungus-free, and had only recently fallen to the ground, they would have been preferred as oviposition sites by gravid *N. arizonensis* females. Such a bias in sampling could have occurred if a large number of fungus-free 'tree pods' fell to the ground shortly prior to pod collection.

Kistler (1985) reported that *A. prosopis* was the most common mesquite bruchid in a guild of the following four bruchid species in Arizona: *A. prosopis*, *Mimosestes amicus*, *N. arizonensis* and

M. protractus. *Neltumius arizonensis* was considered to be rare in Arizona. Kistler (1985) compared the seasonal abundance of these four bruchid species with mesquite pod phenology in Arizona. The following conclusion was drawn: *Algarobius prosopis* first emerges early in the season from green, immature pods. Subsequent generations of this species utilize dry pods, and its population size declines late in the season. *Neltumius arizonensis* first emerges when pods are already dry, approximately two months after *A. prosopis* has made its first appearance. The present study reports a similar sequence of events.

Reasons for the numerical dominance of *A. prosopis* in Arizona may include the following (Kistler, 1985):

1) *Algarobius prosopis* larvae develop more rapidly, and adults live longer, than those of other bruchid species that occur sympatrically with it. The physiology of *A. prosopis* larvae and adults is less affected by temperature than that of other bruchid species;

2) *Algarobius prosopis* suffers less severe temperature-related egg mortality than other bruchids do, because it inserts its eggs into cracks in the pod mesocarp. In contrast, *Neltumius arizonensis* cements its eggs to the pod surface. For this reason, *A. prosopis* is also less susceptible to egg parasitism.

3) The larvae of *A. prosopis* are highly mobile, whereas those of *N. arizonensis* exhibit a low propensity to move. Suitable seeds in which to develop are therefore sought by ovipositing females and by larvae in *A. prosopis*, but only by ovipositing females in *N. arizonensis*.

In South Africa, the higher frequency of *A. prosopis* emergence from mesquite pods may simply be attributed to the fact that this species was released five years before *N. arizonensis*.

Interference by native parasitoids

In Arizona, parasitic Hymenoptera (larval parasitoids) strongly influenced the dynamics of bruchid populations. Up to 50% of the bruchid larvae in thirty mesquite pods were parasitized by species of Braconidae, Eulophidae, Eupelmidae and Eurytomidae (Kistler, 1985). Although two species of eupelmids, a pteromalid species and a eulophid species appear to have adopted the bruchids introduced into South Africa as hosts, the rate of larval and pupal parasitism is negligible. The rate of parasitism of *A. prosopis* and *N. arizonensis* larvae and pupae reported earlier, 0.83%, is comparable with the rate of *A. prosopis* parasitism reported by Hoffmann *et al.* (1993a) (0.4%).

The conclusion that larval and pupal parasitism of the introduced bruchids is negligible, was based on counts of adult parasitoids and bruchids. This method ignored the possibility that indigenous, African parasitoids may well have parasitized large numbers of bruchid larvae, but that the physical structure of the exotic, North American mesquite pods prevented the successful emergence of wasp progeny. It was for this reason that 126 seeds were soaked in alcohol for the purpose of softening, and dissected to reveal the bruchid larvae inside. Only one parasitoid pupa was found associated with what looked like the remains of a parasitized bruchid larva (Plate 3). Fifty-one seemingly unparasitized bruchid larvae were found in these seeds.

Examples of "biotic interference" with insects imported for biological weed control abound (Goeden and Ricker, 1970; Surles, 1974; Goeden and Louda, 1976; Müller and Goeden, 1990; Julien, 1992; Hill and Hulley, 1995). Cornell and Hawkins (1993) reported that the general rate of parasitoid attack of introduced insect herbivores is lower than that of native herbivores. Introduced herbivores are more often attacked by generalist parasitoids than by specialists, and although the species richness of parasitoid complexes on introduced herbivores shows a weak tendency to increase in one hundred and fifty years, the ratio of generalists to specialists does not change (Cornell and

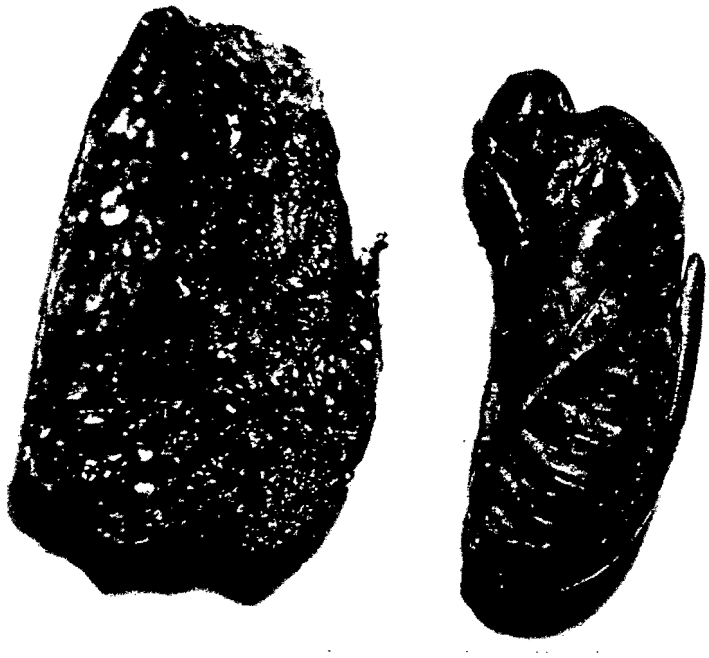


Plate 3 Remains of bruchid larva (left); pupa of chalcidoid wasp (right)

Hawkins, 1993). Generalist parasitoids are less able to regulate populations of their hosts than are specialists (Hassell, 1978). The consensus seems to be that introduced biological weed control agents are not usually affected to a debilitating degree by native parasitoids that have undergone host shifts (Goeden and Louda, 1976; Hill and Hulley, 1995).

Seed damage

Kistler (1985) reported that individual trees in the same site in Arizona suffered different degrees of seed predation. There was a positive relationship between the percentage seeds destroyed by bruchids, and the percentage good (viable) seeds per pod and per tree: variability in resource quality limited seed predation by bruchids on mesquite in Arizona.

Furthermore, Kistler (1985) detected an alternate year pod production pattern in Arizona mesquite. Trees that produced large numbers of pods in a good year produced few or no pods in the previous year and in the succeeding year. In extending this

analysis, Kistler (1985) wrote that trees that produced large numbers of pods and good seeds had a greater number of seeds killed by bruchids - "If the previous year was good then the present year will usually be poor in seed production, and seed predation will also be poor". The above analysis may explain why the present study recorded lower seed damage levels in 1995 than in 1994.

CHAPTER 4: GENERAL DISCUSSION AND CONCLUSIONS

The following questions are pertinent in addressing the biocontrol effectiveness of the bruchids introduced onto mesquite in South Africa:

1) How successful is *N. arizonensis* likely to be as a biocontrol agent of mesquite in South Africa?

2) Can seed-feeding insects influence the dynamics and densities of perennial weed populations?

3) Have seed-feeding insects been used successfully against other perennial weeds?

4) What other phytophagous insects, excluding seed-feeders, may be promising biological control agents for mesquite in South Africa?

HOW SUCCESSFUL IS *N. arizonensis* LIKELY TO BE, AS A BIOCONTROL AGENT OF MESQUITE IN SOUTH AFRICA?

Four factors point to the answer of this question:

i) The results of this study suggest that *N. arizonensis* populations are currently too small to have a marked effect on mesquite.

ii) *Neltumius arizonensis* populations peak only after the vast majority of mesquite pods have fallen to the ground. The particular function of *N. arizonensis*, that is, destroying seeds before they become available to grazing mammals, is not being performed.

iii) It is possible that rainfall limits the growth of *N. arizonensis* populations, by rendering pods on which fungi have grown, unsuitable for oviposition. This phenomenon may, however,

be limited to areas in which high volumes of rain fall. Where mesquite infestations are at their densest, in the north-western Karoo, conditions may be dry enough to suit the fungus-free pod requirements of *N. arizonensis*.

iv) The conclusion that the parasitoid, *Uscana* sp. does not affect *N. arizonensis* adversely, may be premature. High rates of parasitism were recorded at Onderplaas in 1994 and 1995, and at Clanwilliam in 1994. Piketberg, the wettest of the three sites visited in this study, appeared to be free of trichogrammatids. The examination of mesquite pods from Molopo, bordering on the Kalahari Desert, yielded rates of egg parasitism up to 20% (J.H. Hoffmann, University of Cape Town, pers. comm.). It is possible that *Uscana* sp. occurs more frequently in arid areas, and that its importance has been underestimated in this study.

CAN SEED-FEEDING INSECTS INFLUENCE THE DYNAMICS AND DENSITIES OF PERENNIAL WEED POPULATIONS?

According to Janzen (1969) plant ecologists in the nineteen-sixties argued that plants produce so much seed that variation in seed mortality is unimportant: the "Prodigal Parent Theory" asserted that only one seed has to survive to produce another plant. From the results of his studies on tropical legumes and bruchid beetles, Janzen (1969) found support to counter this, and he suggested that the production of a large number of seeds is an evolutionary response to seed predation. But Anderson (1989) stressed the importance of distinguishing between the effects of seed predation on the reproductive success of individual plants (which may result in evolutionary changes in seed morphology, for example), and the notion that insect seed predators influence the recruitment and dynamics of plant populations.

Harper (1977) suggested that any degree of seed damage could result in a lower rate of plant population increase, but that a plant species-dependent threshold degree of seed damage would have to be incurred before plant population density would be

affected. Flower- and seed-feeding insects were the primary factors limiting the recruitment and abundance of the perennial *Haplopappus squarrosus* (Asteraceae) along a climatic gradient in California (Louda, 1982).

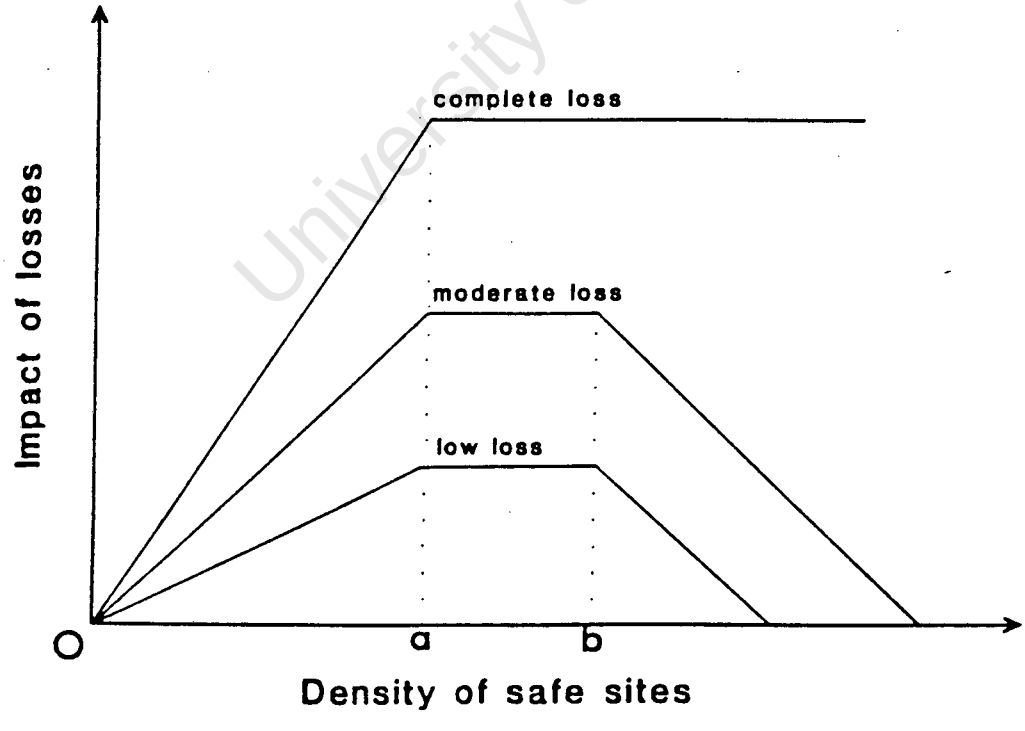
According to Anderson (1989), however, the importance of seed loss to plant population recruitment and the rate of population increase, is related to the availability of safe sites for germination (Figure 4.1). Seed predation is irrelevant when safe sites are absent, (because later, density-dependent seedling mortality is high), negligible when safe sites are rare, and greatest when safe sites are so numerous that recruitment is limited by seed supply. Anderson (1989) used, as corroboration of this theory, his experimental determination that recruitment in the long-lived perennials, *Eucalyptus baxteri*, *Leptospermum juniperum* (Myrtaceae), *Casuarina pusilla* (Casuarinaceae) and *L. myrsinoides*, was unaffected by 95% seed loss, and that it was determined, rather, by the rarity of safe sites. In another study, Louda (1983) concluded that recruitment in *H. venetus* was limited by differential seedling mortality along the same climatic gradient in which *H. squarrosus* recruitment was seed-limited.

That seed predators affect the dynamics and densities of natural populations of perennial plants is clearly not easily demonstrated, even in the light of logical arguments such as those outlined above. Paynter *et al.* (1996) reported that the accumulation of Scotch broom (*Cytisus scoparius* Link (Fabaceae)) seed banks could only be restricted by very high levels of seed predation by *Bruchidius villosus* F (Bruchidae) in Australia. They introduced additional variables into the debate. According to Paynter *et al.*, the influence of seed predators is affected by the level of seed production and the type of seed dispersal involved. Scotch broom stands shaded by *Eucalyptus* forest produce a smaller seed crop than Scotch broom stands in open pasture, and the former are likely to be affected by the same reduction in seeds to a greater extent than open pasture stands. Furthermore, Paynter *et al.* (1996) predict that the invasive vigour of plants that disperse seed by vectors will be curbed

more effectively by seed predation than that of plants that disperse seed ballistically by pod dehiscence.

Cytisus scoparius is not only the target of biological control in Australia and New Zealand. In Oregon, USA, *Exapion fuscirostre* F regularly destroys 85% of *C. scoparius* seeds, but has neither controlled broom nor halted its spread (Andres and Coombs, 1992; cited by Paynter *et al.*, 1996).

FIGURE 4.1 Generalized model of the impact of seed losses on plant population size, viewed as a function of the density of safe sites (reproduced from Anderson, 1989).



HAVE SEED-FEEDING INSECTS BEEN USED SUCCESSFULLY AGAINST OTHER PERENNIAL WEEDS?

Nine species of the plant family Mimosaceae have been the targets of biological control using seed-feeding insects (Julien, 1992). Seven of these occur in South Africa.

In 1982 the pteromalid, *Trichilogaster acaciaelongifoliae* Froggat was released against *Acacia longifolia* (Andrews) Willdenow, an Australian plant that is a weed in South Africa. Dennill and Donnelly (1991) reported that pod production is reduced by between 89% and 95%, when flower buds on more than 50% of branches are galled by this wasp. Galls induced by *T. acaciaelongifoliae* also suppress vegetative growth, causing higher abscission rates of mature phyllodes, shoot die-back and a decrease in lateral branching (Dennill and Donnelly, 1991).

In 1985 the curculionid, *Melanterius ventralis* Lea was released in South Africa to destroy the seeds of *A. longifolia* that developed from flowers which escaped galling by *T. acaciaelongifoliae*. Although the spread of this weevil was reported to be slow, seed damage levels between 14.9% and 79.5% were recorded three generations after its release. The efficient location of pods by *M. ventralis*, even at low pod densities, alleviates any adverse effect of the reduction in pods by *T. acaciaelongifoliae* (Dennill and Donnelly, 1991).

The curculionid, *Melanterius acaciae* Lea was released in South Africa against the Australian *Acacia melanoxylon* R. Brown, in 1986. Low levels of seed damage (0.1% to 3.1%) were recorded in 1989. The reproductive phenology of *A. melanoxylon* appears to determine the survival and dispersal of its biocontrol agent: when fruiting is biennial and synchronous, weevils do not survive. When pods are produced annually, and when pod production is biennial but asynchronous, weevils survive and disperse (Dennill and Donnelly, 1991).

Release of *Melanterius servulus* Pascoe against *Paraserianthes lophantha* (Willdenow) Nielsen [formerly *Albizia*

lophantha (Willdenow) Bentham] was postponed until 1989. In that year it was demonstrated that *M. servulus* could be chemically controlled on the commercially important seed orchards of *Acacia mearnsii* De Wild., on the seeds of which it was able to develop (Dennill and Donnelly, 1991). In 1993 *Melanterius maculatus* Lea was released against *A. mearnsii* and in 1994 *M. servulus* was deployed on *Acacia cyclops* A. Cunn. ex G. Don. It is too soon to tell whether or not these recently released agents will significantly reduce the sizes of their respective host seed crops (D. Donnelly, Plant Protection Research Institute, South Africa, pers. comm.).

Acacia nilotica indica (Bentham) Brenan and *Mimosa pigra* Linnaeus, of Indian and Tropical American origin, respectively, are weeds in Australia: the latter species is also a problem in Thailand and Vietnam (Julien, 1992). Fifty-two per cent and 30% of *A. n. indica* seeds are destroyed by the bruchids, *Bruchidius sahlbergi* (Schilsky) and *Careydon serratus* (Oliver), respectively, where seeds are not grazed by livestock in northern Queensland (Willson, 1985). The bruchids, *Acanthoscelides puniceus* Johnson and *A. quadridentatus* (Schaeffer) are unlikely to affect stands of *M. pigra* in Australia where seed production is strongly seasonal. In the early 1990's these bruchids together destroyed 25% of seeds in Thailand, but their establishment in Vietnam has not been confirmed (Julien, 1992).

The average time, until the present, spent in the field by seed-feeding biological control agents of mimosaceous weeds in South Africa, is about 6 years. On an ecological time scale this represents a very short period. Assessment of the ability of these insects to destroy annual seed crops is further hampered by the various insect species having experienced different times of release, and different durations in the field, and by the idiosyncratic weed and insect phenologies involved.

In evaluating the biological control programmes mentioned above, it is important to consider the context surrounding each weed species. Seed-feeding insects are desirable in biological weed control when: 1) the candidate weed is at an early stage of

invasion: It is hoped, for example, that *Acanthoscelides macrophthalmus* (Schaeffer) will soon be released against *Leucaena leucocephala* (Lam.) De Wit, still considered a potential weed problem (S. Neser, Plant Protection Research Institute, South Africa, pers. comm.), and 2) conflicting interests prevent the introduction of other, more destructive agents, as in the case of mesquite (Neser and Kluge, 1986) and the two australian *Acacia* species that are economically important to forestry, and for fuelwood (Dennill and Donnelly, 1991).

Probably the most well known example of biological weed control using a seed-feeding insect is the programme against Gorse, *Ulex europaeus* Linnaeus (Fabaceae). In 1926 the weevil, *Apion ulicis* (Forster) (Apionidae) was released in Hawaii, but it did not establish at that time (Julien, 1992). In the 1950's *A. ulicis* was re-released in Hawaii, with two additional agents, the gall-forming *A. scutellare* and an unidentified *Apion* species. Only *A. ulicis* became established, attacking 52% of Gorse pods on the island of Maui in 1984. *Apion ulicis* was less successful on the island of Hawaii, where a Gorse control program eliminated the insect in the 1970's. It was re-introduced in 1984 and has re-established there (Markin and Yoshioka, 1989).

Gorse has also been the target of biological control in the USA, where it invades pastures and rangeland in the coastal counties of California, Oregon and Washington. *Apion ulicis* was introduced into California in 1953, but gorse plant density has not been reduced despite attack rates as high as 50% of seed pods. For this reason Californian workers have released the gorse spider mite, *Tetranychus lintearius* Dufour (Acari: Tetranychidae), which causes sucking damage to gorse shoots and spines, in four counties (Turner and Pitcairn, 1995).

Apion ulicis was established in New Zealand in 1931, and in Australia in 1939. Estimates of seed destruction in New Zealand range from 20% to more than 90%, and though *A. ulicis* seems to be effective there, Australian workers report that the rate of spread of gorse has not been reduced in that country.

Attempts at evaluating the biocontrol effectiveness of insects released on gorse, among other globally-distributed weeds at which seed-feeders have been directed, have been lacking or comprised simple estimates of the amount of seed destroyed (Harley, 1985). Though studies of the latter type, and such as the present work on mesquite, are necessary, long-term research should progress beyond this, to examine the effect of seed destruction on the population dynamics of weeds. Ending research programmes after determining only the extent of seed damage will not resolve the question of whether or not seed-feeding insects can be effective in biological weed control.

WHAT PROSPECTIVE PHYTOPHAGOUS INSECTS, EXCLUDING SEED-FEEDERS, MAY BE PROMISING BIOCONTROL AGENTS FOR MESQUITE IN SOUTH AFRICA?

Considering the discussion above, it may be reasonable to suggest that the introduction of insects more directly damaging to mesquite than seed-feeders, may result in a higher degree of mesquite control. Of all the potential mesquite biological control agents, stem-boring insects may ultimately achieve the highest degree of control. This contentious issue is addressed later. Similarly, mesquite foliage feeders could be effective. But the next step forward for mesquite biological control which is most likely to be acceptable to proponents of mesquite utilization, involves not these insects, but, firstly, those which attack immature pods, and later those which destroy flowers (Figure 1.2).

Although flower- and seed-feeding have been treated as a single mode of attack in the question of insect influence upon plant populations (Louda, 1982), in the case of mesquite biological control flower-feeders may be more effective than seed-feeders: the destruction of one mesquite flower destined for pollination may result in the prevention of development of up to thirty seeds. Amidst fears of interspecific agent competition, Hoffmann and Moran (1992) reported that the seed-feeding curculionid, *Rhyssomatus marginatus* Fåhraeus, destroyed up to 88% of *Sesbania punicea* seeds that developed after as many as 98% of

flower buds had been eaten by *Trichapion lativentre* (Beguin Billecocq), another biological control agent of the weed. As with *M. ventralis*, efficient pod location by *R. marginatus* allowed it to complement the effect of *T. lativentre*.

A checklist of insects found on mesquite in the Americas was compiled (Ward *et al.*, 1977), and Cordo and DeLoach (1987) listed insects that attacked mesquite in Argentina and Paraguay. After elimination of insects that were incidentally associated with mesquite, the latter authors concluded that 77 phytophagous species were of possible value as biocontrol agents of mesquite in the USA. The following discussion highlights some insects that featured prominently in the literature.

Pod-feeders

According to DeLoach (1988, 1992) the coreid, *Mozena obtusa* Uhler was effective in damaging young mesquite spikes, pods and tender stems, but its specificity has not been tested. Lepidoptera that fed internally in mesquite pods included the lycaenid, *Strymon leda*, the olethreutids, *Ofatulena spp.*, the notodontid, *Didigua argentilinia* and the cocthylid, *Phalonia leguminana* (DeLoach, 1988).

Bud-feeders

The lepidopterans, *Callipropra sexstrigella* (Chambers) (Gelechiidae), *Ithome concolorella* (Chambers) (Walshiidae) and *Leptotes* sp. (Lycaenidae) inflicted considerable damage upon mesquite buds (Rogers, 1976). *Sibinia sulcatula* (Casey) (Curculionidae) (Rogers *et al.*, 1975) and the cecidomyiid, *Asphondylia prosopidis* Cockerell (Rogers, 1973; cited by DeLoach, 1992) also fed on mesquite buds. The latter species was considered a promising candidate for South Africa by DeLoach (1992).

Foliage-feeders

Melipotis indomita Walker (Noctuidae) has been well studied.

This caterpillar caused complete defoliation of mesquite (Cuda *et al.*, 1990; DeLoach, 1994; Ueckert, 1974), but also fed on the foliage of other legumes (DeLoach and Cuda, 1993). The geometrid, *Semiothisa cyda* (Druce), the gelechiid, *Friseria cockerelli* (Busck) and the pyralid, *Tetralopha euphemella* Hulst appeared specific to three or four *Prosopis* species, including the South African weeds, *P. velutina* and *P. glandulosa* (DeLoach, 1983; DeLoach, 1981 and DeLoach, 1982 respectively). Unlike *M. indomita*, the diurnal feeding habits of these moths may render them susceptible to predation (DeLoach, 1983).

Stem-borers

It is doubtful whether certain stem borers that were recorded on mesquite in the USA should be considered for mesquite biocontrol in South Africa: only stem-boring insects whose damage is confined to mesquite stems less than 1cm in diameter, or to sapling plants, should be considered for introduction (Moran, 1991). Probably, the shade offered by any *Prosopis* species in South Africa will be the weed's last desirable attribute to be sacrificed, if ever it is, in order to effect mesquite control.

The host specificity of *Megacyllene robusta* Linsley and Chemsak (Cerambycidae) (Linsley, 1964) has not been tested, and it was feared that this species may attack large mesquite branches of mature trees. The cerambycids, *Oncideres rhodosticta* Bates (Ueckert *et al.*, 1971) and *O. cingulata* (Say) (Rogers, 1977) girdled mesquite branches 0.5 cm to 2.0 cm in diameter, while *Aneflus protensus* (LeConte) (Cerambycidae) fed in the main trunk (Linsley, 1963). The curculionid, *Colecerus marmoratus* Horn. was abundant on *P. glandulosa* in Texas, but its feeding behaviour and host range have not been studied. Other short-nosed weevils that are potential candidates are root feeders (DeLoach, 1988), and would presumably be as destructive as stem-borers that attack large branches.

CONCLUSIONS

Neltumius arizonensis did not measure up to the performance of *A. prosopis* at three sites in Western Cape:

1) *Neltumius arizonensis* egg densities were low.

2) Levels of *N. arizonensis* emergence were up to eighty-six times lower than those of *A. prosopis*.

Reasons for the infrequent oviposition and low population levels of *N. arizonensis* include:

1) the preference of *N. arizonensis* for clean, tree-borne pods as oviposition sites, to the relative exclusion of those lying on the ground and covered in fungus,

2) its late release, compared to the release of *A. prosopis*,

3) interference by trichogrammatid egg parasitoids,

4) the life-history of *N. arizonensis* (low fecundity and the high degree of specialization of adults and larvae, compared to *A. prosopis*).

A follow-up investigation of egg density (particularly on 'tree pods' when these are abundant in January, February and March) and emergence of *N. arizonensis* should be conducted. This will establish whether or not the purported influence of egg parasitoids on *N. arizonensis* will increase with intensity as time passes, and whether or not *N. arizonensis* populations are likely to grow in the future. The results of this study suggest that *N. arizonensis* will not effectively perform the function for which it was intended in the South African mesquite biocontrol programme.

The results of this study may be interpreted in a dual manner: from the viewpoint of those who consider mesquite purely as an aggressive weed, and from the perspective of the mesquite

utilizer who wishes to manage the plant.

Probably the former will be disappointed by this report, because it illustrates that current levels of seed damage are too low to reduce the density of existing mesquite infestations. Even the rate of spread of mesquite may not be slowed by the bruchids, particularly where strict livestock management and pod harvesting are not practised. But the reduction in size of dormant mesquite seed banks by the introduced bruchids, should salvage their reputation in the eyes of mesquite opponents. Bruchid populations are likely to grow in the future, and damage more seeds than the numbers recorded in this study.

The farmer who values mesquite pods as fodder but wants to check the weed's spread, will be more optimistic on reading this. If pods are harvested and stored, out of the reach of livestock and protected from the elements, they may be used as fodder. The few seedlings that sprout in enclosed livestock feeding-camps may be controlled manually.

Although theoretically feasible, the above scenario may be impractical on large farms. Moreover, it is the aim of biological control to lessen the need for other forms of weed control. It can be argued that mesquite biocontrol workers have not had free rein in the past decade. The introduction of seed-feeders was all that could be done to curb the weed's spread. Now that more farmers have decided that pods are superfluous as fodder in the face of the negative consequences of their use as such, additional biocontrol agents may be introduced. Pod-feeding insects are especially good candidates. With them it may be possible to prevent the physiological development of seeds, without affecting the use of mesquite flowers for apiculture. Flower-feeding insects may prove to be even more effective than pod-feeders, providing their impact on bee-keeping is assessed first. Because *A. prosopis* is host-specific, and presumably has good pod-locating abilities, it may co-exist with a pod- or flower-feeding agent. The introduction of foliage- or stem-feeding biocontrol agents should be seen as a last resort in mesquite biocontrol.

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