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Combined effect of natural enemies (Hymenoptera: Aphelinidae & Coleoptera: Coccinellidae) with different niche breadths in reducing high populations of red scale, *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae)

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Abstract

Three populations of *Aonidiella aurantii* (Maskell) were studied on orange trees at two sites in the hot Transvaal lowveld in South Africa. The first two were on the same trees, which had severe scale in the tree crowns and a low infestation in the bottoms. The third population, at a second site, was high and relatively evenly-spread over the whole tree. In previous years, the parasitoids *Aphytis africanus* Quednau and *A. melinus* DeBach had been unable on their own to reduce the high scale populations. Once a certain scale density level on the tree framework had been breached, a proportionately large number of susceptible scales escaped parasitism and reached the gravid female stage, which is invulnerable to attack. The ineffectiveness of parasitoids in these circumstances, resulting partly from their narrow niche breadth, was compounded by peak numbers only being reached late in the season. By this time, the large number of adult scales had already rendered the fruit unmarketable. In both sites, the predator *Chilocorus nigritus* (F.) was introduced and the trees also received commercial applications of petroleum oil. In one site, this oil treatment was restricted to the tree crowns. Although overall parasitism of vulnerable stages was relatively unaffected by these abiotic and biotic controlling factors, there was a shift to increased percentage parasitism of the virgin female away from the other susceptible stages. In addition, it was confirmed that the broad attack niche provided by *C. nigritus*, which preys on all developmental stages of the scale, readily complements parasitoid activity and can be of major economic importance.

Introduction

At altitudes of 1000–1300 m in southern Africa, *Aphytis africanus* Quednau is effective in maintaining red scale, *Aonidiella aurantii* (Maskell), at low population levels (Bedford, 1968; Catling, 1971). In the hotter lowveld (200–800 m) however, this species and *Aphytis melinus* DeBach are not such efficient regulators (Atkinson, 1977). This is largely because *Aonidiella aurantii* generation turnover is more rapid at the higher temperatures, and

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parasitoid population increase is possibly limited by high summer temperatures (Atkinson, 1983; Catling, 1971). Behavioural factors also play a role. At high host levels, the parasitoids are inversely density-dependent within a patch the size of a fruit or smaller (Samways, 1985, 1986). The net effect of these climatic and behavioural factors is that large numbers of immature individuals of *A. aurantii* escape parasitism early in the season to become long-lived, invulnerable gravid adults. These females then produce localized high-density patches of offspring, which, in economic terms, are unacceptable.

The aim here was to study parasitism rates at high, declining, and at low host levels. Reductions were achieved using an abiotic factor (petroleum oil), and an additional natural enemy (*Chilocorus nigritus* (F.)) with a rapid functional and numerical response and a niche breadth much wider than that of the parasitoids.

Sites and methods

Sites

Two sites were used. They were chosen because they both had commercially unacceptably high levels of *A. aurantii* and because both lacked *C. nigritus* as a member of the natural enemy complex.

The first site was near Nelspruit, South Africa, and was composed of 4–6-m high Valencia sweet orange trees (*Citrus sinensis*) with a severe infestation of *A. aurantii* in the tree crowns but a much lower infestation in the bottom half of the trees. The second site was near Komatipoort, 130 km east of Nelspruit, and was also large Valencia trees but with a severe *A. aurantii* infestation over the whole canopy.

Oil application and predator introduction

On 16 August 1983, the crowns of the Nelspruit trees were treated by hand gun from towers with a narrow distillation range oil (1·2% Orchex). This insecticide was chosen because of its relatively benign effect upon parasitoids (Campbell, 1975). This treatment was carried out by arrangement with the grower to ameliorate the *A. aurantii* population, which was so severe that it was causing twig dieback in the tree crowns. Four trees in the orchard were control trees and were not given the crown treatment. Between 7 December 1983 and 23 February 1984, about 20 000 eggs from insectary cultures of *Chilocorus nigritus* were introduced on polyester fibre pads (Samways & Mapp, 1983) into a block of 25 trees. The remainder of the orchard acted as the control. This species of predator was chosen because of its known behaviour (especially its ability to feed on gravid, adult scales) and highly important economic impact (Samways, 1984) and because it is relatively easy to rear in large numbers (Samways & Tate, 1986).

On 24 November 1983, the whole canopy of the trees at Komatipoort was treated by hand gun from the ground with 1·4% Orchex. This was carried out by the grower for fear of the *A. aurantii* population becoming too severe. Between 8 December 1983 and 15 March 1984, 60 000 *C. nigritus* eggs were introduced into a block of 25 trees within the orchard.

Measuring Aonidiella aurantii *reduction*

At both sites, *C. nigritus* establishment was monitored fortnightly by adult counts within and outside the introduction blocks.

Sampling methods for parasitoids were the same at both sites. Each month, from December 1982 or January 1983 through to July or August 1984, five trees in each site were randomly selected. Two twigs, 150 mm long and with terminal fruit, were taken from each of the four quadrants of each tree at a height of 1·5–2·0 m. The same number of twigs and fruit was taken from the crowns of the same five trees. The number of scales, first moult stage and older (i.e. excluding crawlers and whitecaps), both parasitized and unparasitized, judged to be alive by their external appearance and colour were counted on each whole fruit and twigs. Care was taken not to damage these hosts during examination. The fruit and twigs were then transferred to emergence boxes, where they remained for 20–25 days, to obtain monthly absolute numbers of males of *A. aurantii* and parasitoids.

Economic damage levels were assessed by classifying samples ($n \simeq 500$) of fruit into three *A. aurantii* infestation level categories: zero, 1–9 and >10 mature living adults per fruit.

Percentage parasitism at the Nelspruit site

Experimental comparison of parasitoid activity in the field at high and low host densities is hampered by a complex of biotic and abiotic variables many of which cannot be fixed at the same time. However, the Nelspruit site in 1983 provided an ideal opportunity for comparison of parasitoid activity, because *A. aurantii* levels were high in the tree crowns and low in the lower part of the tree. The only major difference was a microhabitat difference, but all other large-scale variables associated with a study of parasitoid behaviour in the field were overcome. Individual scales were examined to supplement the emergence box results, which only related to males.

Monthly samples of 40 fruits from the tree crowns and 40 from the tree bottoms were taken for stereo-microscope examination. At the beginning and end of the season, all scales on the fruit were counted and their covers lifted. In the middle of the season, when scale density was high, only a representative sample was taken from each fruit, so that the total number of scales examined was at least 500, but usually over 1000, from each batch of 40 fruits. To avoid bias, these representive samples involved examination of every living scale within a whole microscope field of view at 60× magnification. After studying all the scales in a field, the fruit was turned and all those in the next field examined until a satisfactory sample size was obtained.

Results

Nelspruit

The winter oil applied from towers had an unexpectedly high impact on the *A. aurantii* population in the tree crowns, with encrustations of dead individuals falling off the twigs. The tree response was substantial, with vigorous growth that changed the shape of the tops of the trees from flat to pointed. The control trees suffered twig dieback.

After the oil application, the differential in host levels between the tops and bottoms of the trees (Fig. 1*A*) decreased substantially and resulted in an overall decline in the *A. aurantii* population (Fig. 1*B*). With a decrease in hosts, the population level of *Aphytis* spp. also declined (Fig. 2).

The decline in host and natural enemy numbers did not alter the ratio between them (Fig. 3). All differences between the two years were non-significant at the 5% level using the Wilcoxon matched pairs test. Combining the months' catches and calculating the ratio reaffirmed the unaltered ratio from one year to the next (Table I). Although the host:parasitoid ratio was not obviously improved, there was nevertheless highly effective parasitoid activity leading to low levels of *Aonidiella aurantii* infestation at the end of the 1984 season (Table II).

TABLE I. *Ratios of the numbers of males of* Aonidiella aurantii *to one* Aphytis *parasitoid captured in emergence boxes throughout the season*

	Nelspruit		Komatipoort	
	1983	1984	1983	1984
Fruit top	2·76	1·48	6·90	5·55
Fruit bottom	1·37	5·00	4·86	7·82
Twigs top	8·49	4·39	2·0	13·0
Twigs bottom	1·15	2·86	5·50	16·50
Fruit and twigs combined	2·51	1·99	5·55	6·49

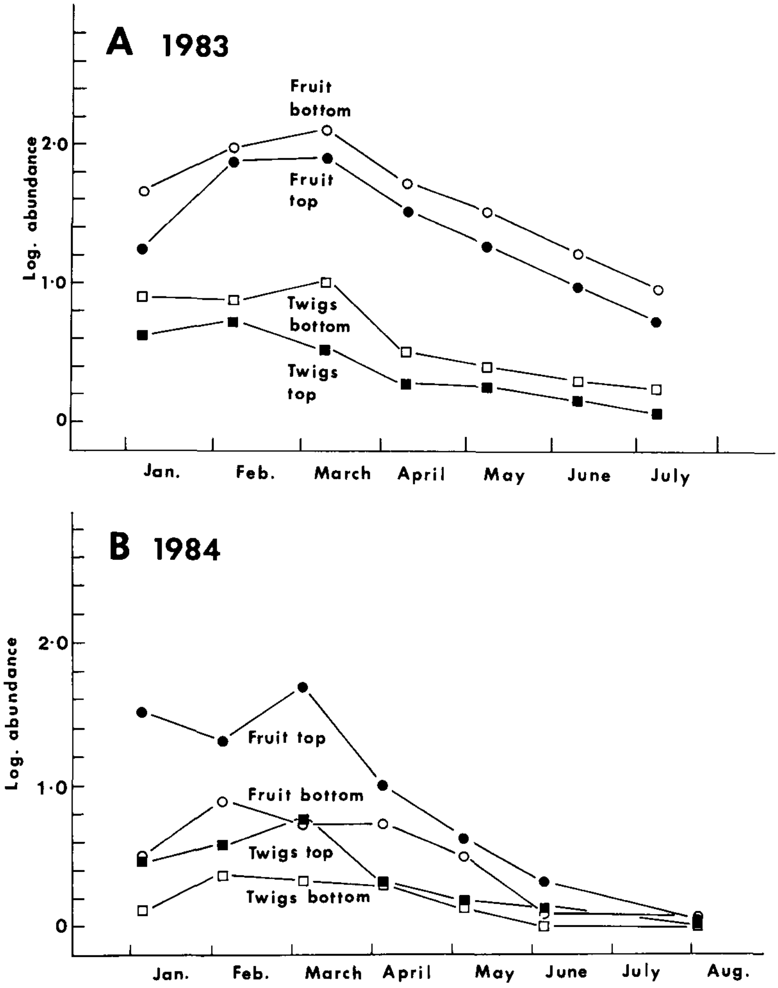

Fig. 1.—Mean log abundance of second-instar nymphs and older individuals of *Aonidiella aurantii* on 40 whole fruits and 40 twigs from the tops and bottoms of citrus trees at the Nelspruit site before (*A*) and after (*B*) tree-crown application of narrow distillation range oil.

Table II. *Percentage infestation of fruit by living gravid females of* Aonidiella aurantii *at Nelspruit*

	1983 (Before oil application)		1984 (After oil application)	
Position in tree	Top	Bottom	Top	Bottom
No. of *A. aurantii* per fruit				
0	16%	53%	69%	71%
1–9	56%	40%	31%	28%
10+	28%	7%	0%	1%

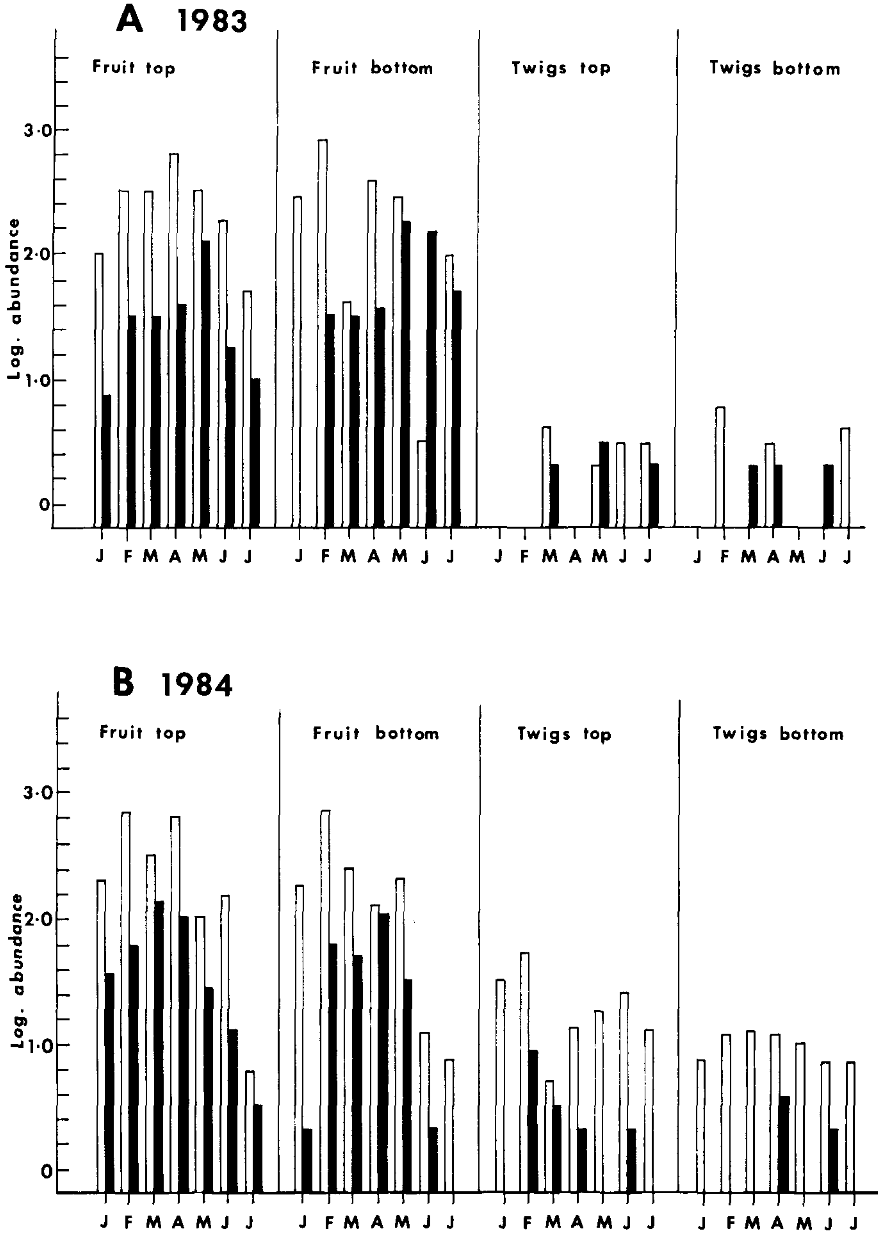

Fig. 2.—Total log abundance of males of *Aonidiella aurantii* (open columns) and *Aphytis africanus* and *A. melinus* (black columns) captured in emergence boxes containing 40 whole fruits and 40 twigs from the tops and bottoms of citrus trees at the Nelspruit site before (*A*) and after (*B*) tree-crown application of narrow distillation range oil.

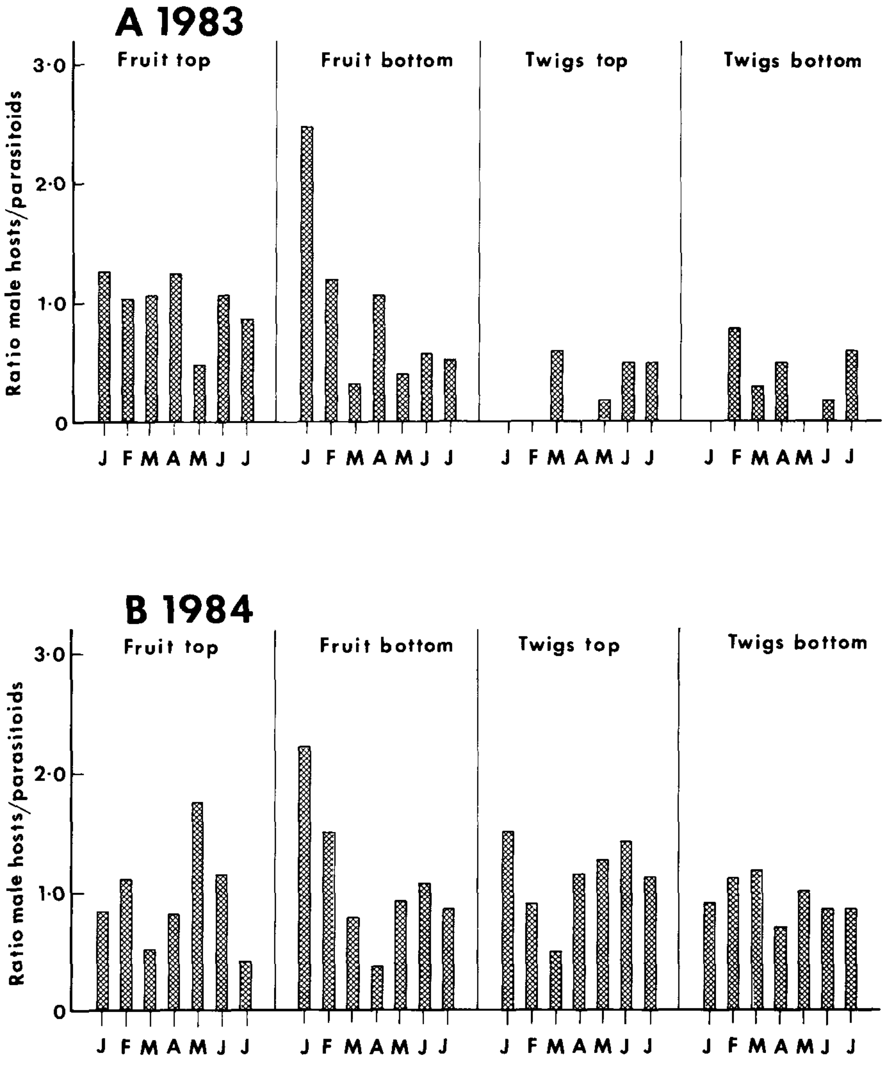

Fig. 3.—Log $(x+1)$ of ratio of males of *Aonidiella aurantii*:adults of *Aphytis africanus* and *A. melinus* on fruit and twigs in the tops and bottoms of trees at the Nelspruit site in (*A*) 1983 and (*B*) 1984.

The impact of the oil application and parasitism was so great that, despite the large input of *C. nigritus* eggs, the predator did not become established. All the beetle counts were zero.

The seasonal patterns of parasitism of *A. aurantii* in the three susceptible stages were similar (Fig. 4). Towards the end of the parasitoid season, there was a greater tendency towards an increased percentage parasitism of the host in all susceptible stages at lower host densities than at high ones. This was particularly the case for virgin adult females.

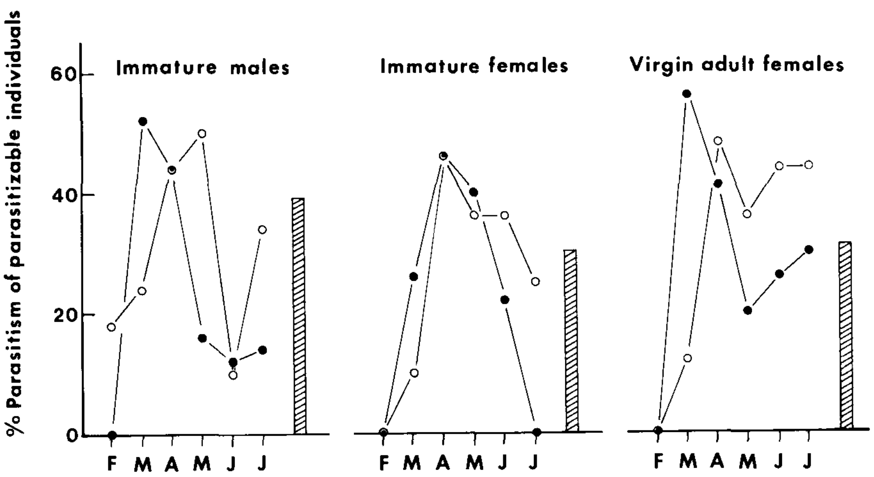

Fig. 4.—Percentage parasitism of parasitizable individuals of *Aonidiella aurantii* at high (●——●) and low (○——○) host population levels at the Nelspruit site. The histograms represent the percentage time window for parasitism of that particular host development stage (i.e. the three stages together = 100%).

Komatipoort

The December oil application mildly suppressed the *A. aurantii* population, but it was insufficient to prevent the scale population from reaching a high level between January and April 1984 (Figs. 5*B*, 6*B*). *C. nigritus* became established well and peaked in May (Fig. 7). At Nelspruit, the oil application came well before the period of parasitoid activity, and from early in the season, parasitoid levels were much the same in 1983 as in 1984. At Komatipoort, parasitoids were abundant early in the 1984 season, just as they were in 1983, but once the impact of the predator was beginning to show, the numbers of parasitoids decreased substantially (Fig. 6*B*). The host numbers also decreased (Fig. 5*B*), so that there was no general decline in host:parasitoid ratio (Fig. 8, Table I).

The economic outcome is not obvious from Fig. 6*B*. However, the combined activity of the predator and the parasitoids resulted in a considerable drop in infestation of fruit at the end of the season, from 48% in 1983 to 0% in 1984 (Table III). This is mainly because, in 1984, *C. nigritus* removed the long-lived gravid adult females which would have otherwise accumulated on the fruit at harvest time as they did in 1983.

TABLE III. *Percentage infestation of fruit by living gravid females of* Aonidiella aurantii *at Komatipoort*

Date of cull analysis	Position in orchard	Infestation level			
		0 *A. aurantii* per fruit	1–9 *A. aurantii* per fruit	10+ *A. aurantii* per fruit	
14 July 1983	Whole orchard	2%	50%	48%	Before *Chilocorus nigritus* introduction
24 April 1984	Experimental block	30%	30%	40%	During *C. nigritus* establishment
24 April 1984	Control	27%	35%	38%	
28 June 1984	Experimental block	76%	22%	2%	
28 June 1984	Control	45%	37%	18%	
2 August 1984	Experimental block	95%	5%	0%	
2 August 1984	Control	76%	19%	5%	
18 July 1985	Whole orchard	97%	3%	0%	After *C. nigritus* establishment

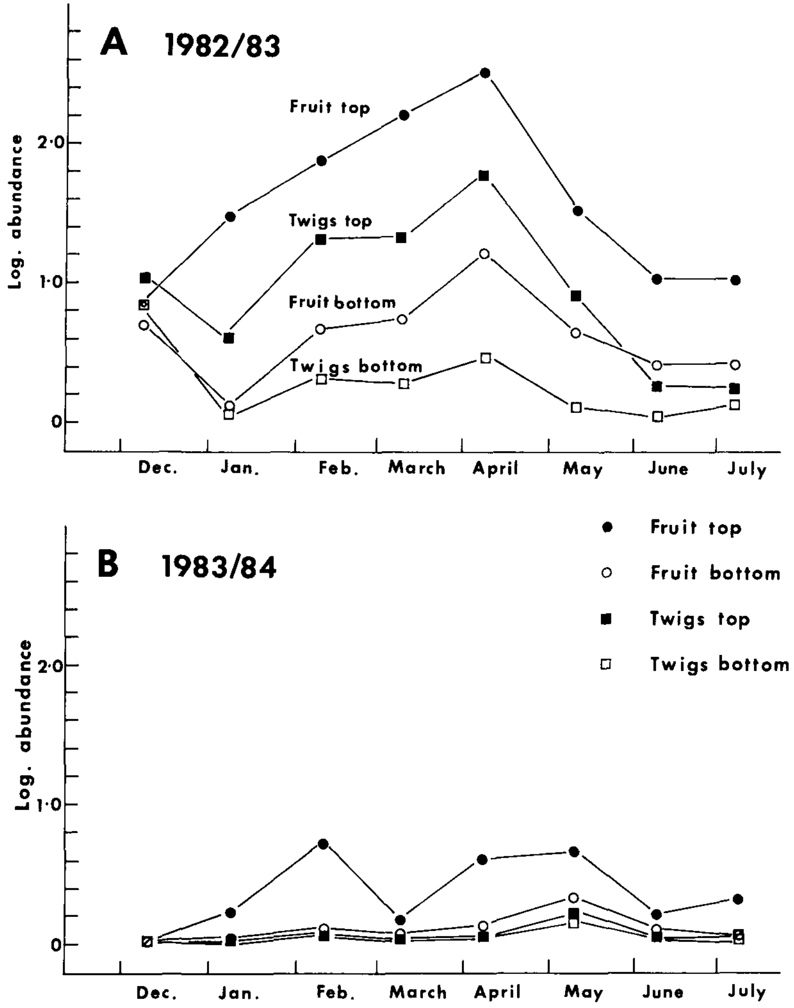

Fig. 5.—Mean log abundance of second-instar nymphs and older individuals of *Aonidiella aurantii* on 40 whole fruits and 40 twigs from the tops and bottoms of citrus trees at the Nelspruit site before (*A*) and after (*B*) introduction of the predator *Chilocorus nigritus*.

During May and June, the beetle dispersed from the experimental block into the rest of the orchard, with the result that in 1984, only 5% of the fruit in the control block was infested with ten or more mature adult females.

After the 1984 decline in *A. aurantii* at both sites, there was no resurgence in 1985 or 1986, the pest being maintained at low levels through the occasional application of oil and combined natural enemy activity. *C. nigritus* became established on several other farms in the area, but its numbers were not quantified. The economic outcome was generally so successful that no insecticidal supplements were required, the predator and the parasitoids together maintaining *A. aurantii* at low population levels.

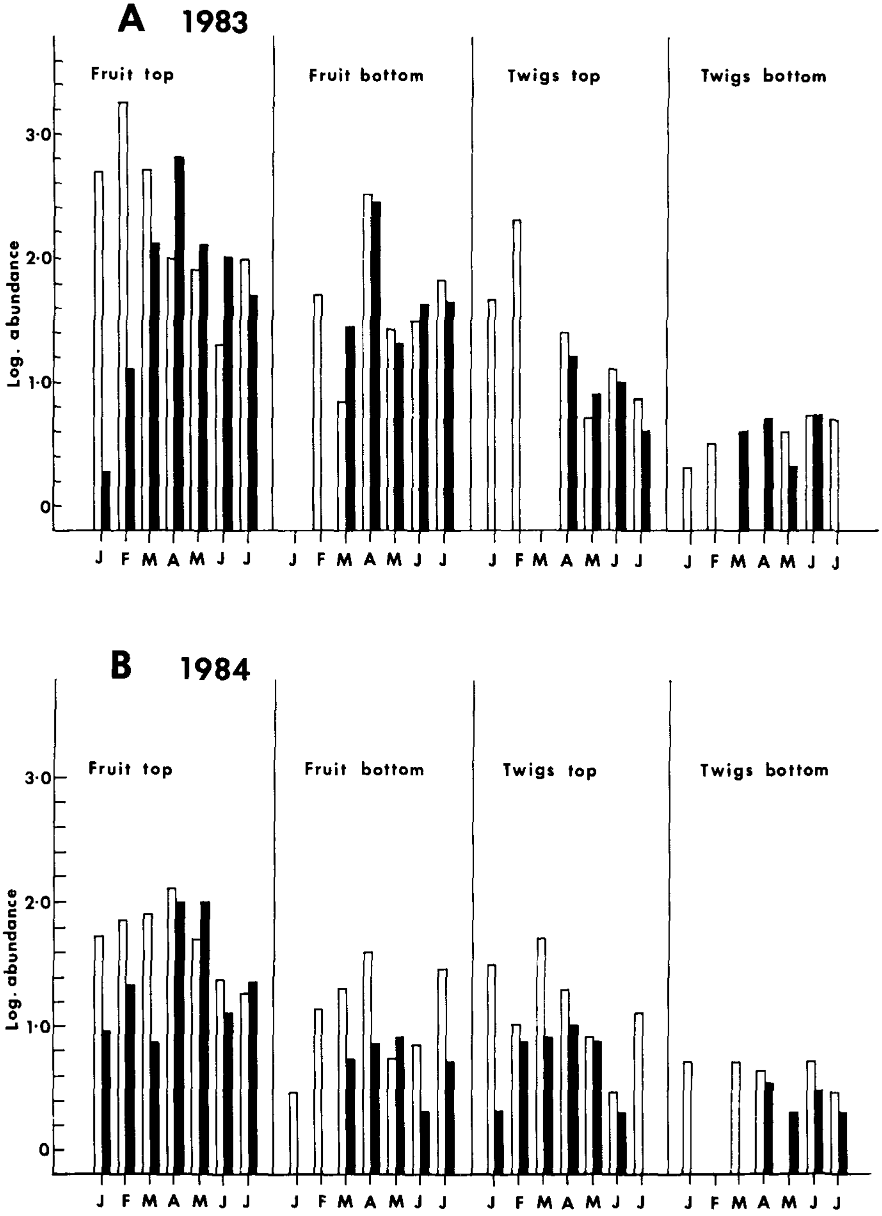

Fig. 6.—Total log abundance of males of *Aonidiella aurantii* (open columns) and adults of *Aphytis africanus* and *A. melinus* (black columns) captured in emergence boxes containing 40 whole fruits and 40 twigs from the tops and bottoms of citrus trees at the Nelspruit site before (*A*) and after (*B*) introduction of the predator *Chilocorus nigritus*.

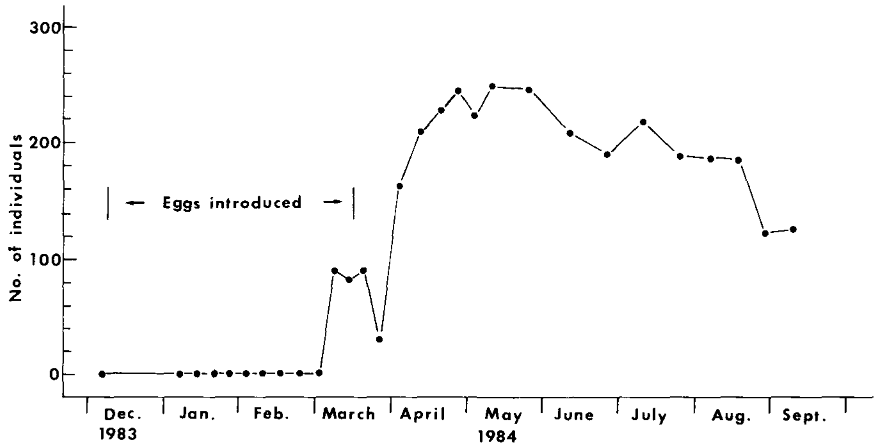

Fig. 7.—Number of adults of *Chilocorus nigritus* established on citrus trees at the Komatipoort site after introduction of eggs of the species.

Discussion

Parasitoid behaviour

At the universe level of fruit and twigs, percentage parasitism was erratic from month to month (Figs. 3 & 8). A severe *A. aurantii* infestation was characterized by an exceptionally high host:natural enemy ratio early in the season (fruit and twigs top in Fig. 3*A* and fruit bottom in Fig. 8*B*). Under conditions of commercial control (as at the end of 1984), there was a significant increase in percentage parasitism, compared with either earlier in that season, or with the previous one when there was unsatisfactory commercial control. Earlier work at these sites has indicated a weak inverse density-dependent relationship between host and parasitoid at *exceedingly* high host population levels (Samways, 1985). Yet no evidence has been found for the converse: that moderate and low population levels are characterized by an increasingly positive density dependence. This is interesting relative to Reeve & Murdoch's (1985) findings that spatial density-dependence could not be invoked as a stabilizing factor in maintaining *A. aurantii* at low level by *Aphytis melinus*. Parasitoid behavioural response therefore apparently changes when the host reaches exceedingly (and unnaturally?) high populations. This is also illustrated by the aggregation of parasitoids at the level of the tree. There is a strong aggregation at very high host levels (Samways, 1986), yet at low host densities, the parasitoid numbers were not a function of host density (Reeve & Murdoch, 1985).

Natural enemy niches

The ratio of male scales to parasitoids remained the same at low as at moderate scale densities. Yet at the end of the season the mature adult female population level was considerably reduced, which was the economic aim. This suggests that there was increasing parasitism at lower densities of the virgin female. This did appear to be the case, particularly later in the season (Fig. 4). Where virgin females escaped parasitism, there was a gradual accumulation of long-lived, mature adult females which constituted an ever-increasing proportion of the host population and characterized a scale outbreak (Samways, 1985). It appears therefore, that parasitism of the virgin adult is crucial to *Aonidiella aurantii* population regulation.

In addition, although the levels of parasitism are similar for the three parasitizable stages, the time window for parasitism of males is only 39% of the total. Thus,

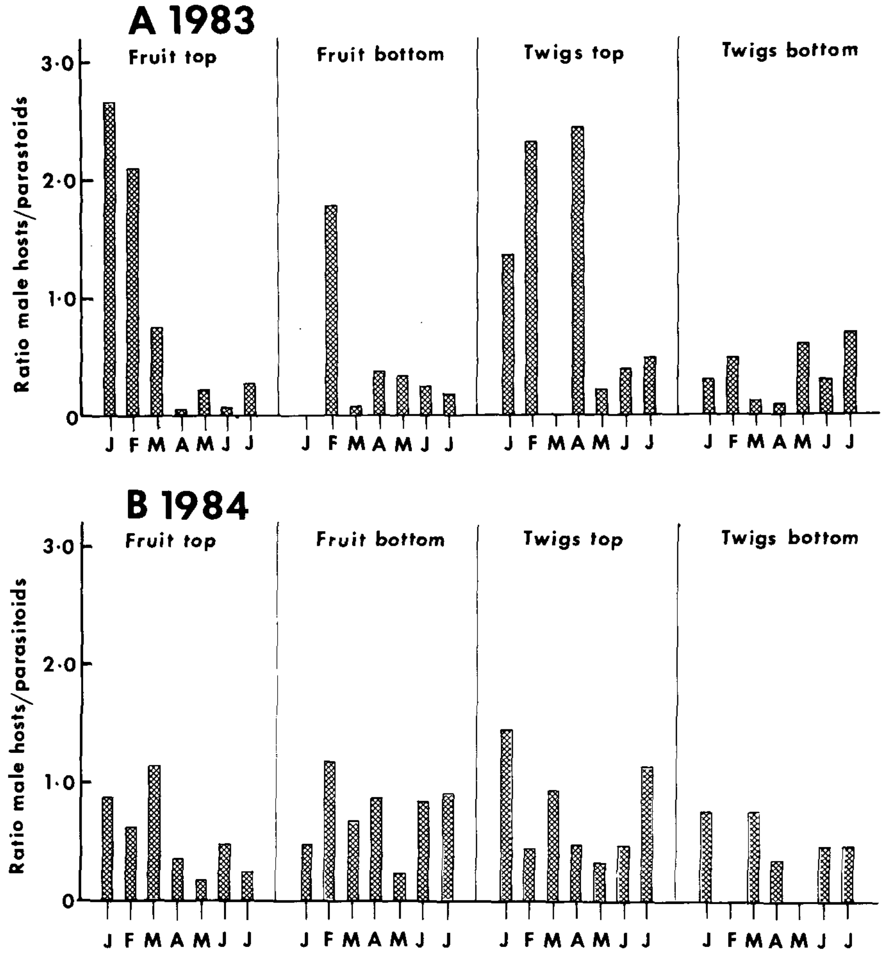

Fig. 8.—Log $(x+1)$ ratio of males of *Aonidiella aurantii*:adults of *Aphytis africanus* and *A. melinus* on the fruit and twigs in the tops and bottoms of trees at the Komatipoort site in (*A*) 1983 and (*B*) 1984.

behaviourally, a single parasitoid may be stimulated to lay preferentially in a male scale, but numerically, there is greater overall percentage parasitism of females, because parasitoid attack on the virgin adult female represents additional parasitism i.e. mortality of survivors from the younger stages.

The importance of *C. nigritus* lies in the fact that it feeds on all sessile stages of the host including the mature adult female. This contrasts with the narrower niche breadth of the parasitoids (their parasitic behaviour and their host-stinging). On establishment, the predator's influence was additive upon that of the parasitoids, and with mortality of the mature adult female, crawler production was halted.

There was strong interference between the parasitoids and the predator. While feeding at dense patches of *A. aurantii*, *C. nigritus* consumed, or at least removed, *all* scales, parasitized as well as unparasitized. Despite this strong interference, the relationship was nevertheless apparently stable and certainly highly detrimental to the host population.

'Escape' from parasitism and suppression with oil

Both this and the earlier study (Samways, 1985) showed an early season 'escape' from parasitism (i.e. the *A. aurantii* population had substantially increased before the parasitoid season had started, leading to unacceptably high scale population levels). The winter oil application in the tree crowns at Nelspruit cleared the fruitless twigs of *A. aurantii* and thus prevented major crawler movement to the fruit in the spring. This reduced insecticide usage yet conserved the pool of parasitoids lower down in the tree. Later in the season, the parasitoids were then able to check any further scale increase. Indeed, the combined effect of the crown applications of oil and the parasitoids was so great that an insufficient number of host individuals remained for establishment of *C. nigritus*. In this vein, Davies & McLaren (1977) speculated that the success achieved in integrating oil and parasitoids was possibly due to insufficient spray application.

At Komatipoort, the oil was applied in the summer after maturation of the first *A. aurantii* generation on the twigs and movement of crawlers to the young fruit. Probably because there were so many scales, particularly adults, the single oil application was unable to reduce this host population to a level where the parasitoids could then efficiently check it. Only then, by introduction of *C. nigritus*, was there late-season control of the scale.

These results in combination with those of Atkinson (1977), Reeve & Murdoch (1985) and Samways (1985, 1986) suggest that spatial and temporal measures of percentage parasitism, and even of parasitoid numbers, are not necessarily good indicators of successful control. Perhaps, axiomatically, it is the net number of host survivors of insecticidal treatments, parasitism and predation combined that determines the economic outcome. With *A. aurantii*, this point is especially important owing to the long-lived virtually invulnerable adult female, which can be attacked if the overall natural enemy resource niche breadth is widened by the addition of a predator such as *C. nigritus*.

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References

ATKINSON, P. R. (1977). Preliminary analysis of a field population of citrus red scale, *Aonidiella aurantii* (Maskell), and the measurement and expression of stage duration and reproduction for life tables.—*Bull. ent. Res.* **67**, 65–87.

ATKINSON, P. R. (1983). Environmental factors associated with fluctuations in the numbers of natural enemies of a population of citrus red scale, *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae).—*Bull. ent. Res.* **73**, 417–426.

BEDFORD, E. C. G. (1968). The biological control of red scale, *Aonidiella aurantii* (Mask.), on citrus in South Africa.—*J. ent. Soc. sth. Afr.* **31**, 1–15.

CAMPBELL, M. M. (1975). Duration of toxicity of residues of malathion and spray oil on citrus foliage in South Australia to adults of a California red scale parasite *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae).—*J. Aust. entomol. Soc.* **14**, 161–164.

CATLING, H. D. (1971). Studies on the citrus red scale, *Aonidiella aurantii* (Mask.), and its biological control in Swaziland.—*J. ent. Soc. sth. Afr.* **34**, 393–411.

DAVIES, R. A. H. & MCLAREN, I. W. (1977). Tolerance of *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) to 20 orchard chemical treatments in relation to integrated control of red scale, *Aonidiella aurantii* (Maskell) (Homoptera: Diaspididae).—*Aust. J. exp. Agric. Anim. Husb.* **17**, 323–328.

REEVE, J. D. & MURDOCH, W. W. (1985). Aggregation by parasitoids in the successful control of the California red scale: a test of theory.—*J. anim. Ecol.* **54**, 797–816.

SAMWAYS, M. J. (1984). Biology and economic value of the scale predator *Chilocorus nigritus* (F.) (Coccinellidae).—*Biocontrol News and Information* **5**, 91–105.

SAMWAYS, M. J. (1985). Relationship between red scale, *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae), and its natural enemies in the upper and lower parts of the citrus trees in South Africa.—*Bull. ent. Res.* **75**, 379–393.

Samways, M. J. (1986). Spatial and temporal population patterns of *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae) parasitoids caught on yellow sticky traps in citrus.—*Bull. ent. Res.* **76**, 265–274.

Samways, M. J. & Mapp, J. (1983). A new method for the mass-introduction of *Chilocorus nigritus* (F.) (Coccinellidae) into citrus orchards.—*Citrus & Subtropical Fruit Journal* no. 598, 4–6.

Samways, M. J. & Tate, B. A. (1986). Mass-rearing of the scale predator, *Chilocorus nigritus* (F.) (Coccinellidae).—*Citrus & Subtropical Fruit Journal*.

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