

Scale Morphology Effects on Feeding Behavior and Biological Control Potential of *Rhyzobius lophanthae* (Coleoptera: Coccinellidae)

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ABSTRACT We compared the morphological characteristics of the scale covers and bodies of 2 economically important scale species, California red scale, *Aonidiella aurantii* (Maskell), and oleander scale, *Aspidiotus nerii* (Bouchè), to determine their protective value against predation by the coccinellid *Rhyzobius lophanthae* (Blaisdell). We also compared the morphology of the mandibles of *R. lophanthae* with that of *Chilocorus cacti* (L.), a specific predator of diaspidid scales. A higher percentage of *R. lophanthae* larvae survived when they fed on 2nd- and 3rd-instar *A. aurantii* and all stages of *A. nerii* than when they fed on gravid and parturient *A. aurantii*. Adult *R. lophanthae* took longer to consume 3rd-instar *A. aurantii* than 3rd-instar *A. nerii* and were frequently unable to penetrate the scale body of gravid and parturient *A. aurantii*. Predator preference for scale stage and species reflected the ease with which it was able to penetrate the scale cover and body of its prey. The hardened scale cover of gravid and parturient *A. aurantii* when coupled with the sclerotized scale body provided the scale with substantial immunity to predation by *R. lophanthae* for approximately two-thirds of the scale life span. We conclude that *R. lophanthae* is unlikely to suppress *A. aurantii* populations below those of economic concern when it is the sole biological control agent present. In contrast, the entire life span of *A. nerii* is vulnerable to predation, and this species appears to be suppressed to low densities by *R. lophanthae*.

KEY WORDS *Rhyzobius lophanthae*, *Aspidiotus nerii*, *Aonidiella aurantii*, feeding behavior, morphology, biological control

Rhyzobius lophanthae (Blaisdell) belongs to a group of predominantly Australian coccinellids that feed on soft scales (Coccidae) (Pope 1981, Gordon 1985). Koebele first discovered this coccinellid in New South Wales, Australia, in 1898 feeding on introduced armored scales (Diaspididae). A consignment of the beetle was shipped to California to aid in the control of *Saissetia oleae* (Bern.) on citrus. Although *R. lophanthae* failed to control this pest, it established in California and subsequently spread throughout the United States feeding on a wide variety of diaspidids (Gordon 1985).

Since its initial introduction into California, *R. lophanthae* has been introduced worldwide as a biological control agent but with mixed success. For example, it has been credited with the control of *Carula spis minima* (Targ.) and *C. juniperi* (Bch.) on juniper in Italy (Greathead 1973), *Chrysomphalus dictyosperimi* (Morg.) on citrus in Morocco (Rungs 1950), *Paralatoria blanchardi* (Targ.) on dates in Israel (Kehat 1967), *Aulacaspis tegalensis* (Zehnt.) on sugar cane in East Africa (Greathead 1973), *Aspidiotus nerii* (Bch.) on citrus and olives in Greece (Argyriou and Kourmadas 1980), and *A. destructor* (Signoret) on coconut in Hawaii

(Beardsley 1970). However, it has failed to control other diaspidid species such as the California red scale, *Aonidiella aurantii* (Maskell). A complete review of these and other introductions is provided by Greathead (1973).

Clausen (1940) hypothesized that the degree of control to be expected from *R. lophanthae* and other scale feeding coccinellids depends on the physical characteristics of the diaspidid cover. Scale species with thin, easily penetrated covers are more likely to be suppressed than those with thick covers. Successful suppression may also depend on factors such as whether a scale stage or species supplies the nutrients or energy necessary for beetle development and reproduction (Muma 1955, Hodek 1973), or whether suitable scale stages are available in sufficient numbers throughout the season to sustain the predator population (Hagen 1974).

We chose to test the Clausen hypothesis (1940) as a first step in evaluating the efficacy of *R. lophanthae* to suppress *A. aurantii*, California red scale, an important pest of citrus in California. To test this hypothesis we compared beetle preference for 2 diaspidid species when given a choice. One of the scale species, *A. aurantii*, had a hard

cover and the other, *Aspidiotus nerii* (Bouchè) oleander scale, had a soft cover. We also compared the following 4 characteristics: (1) handling (consumption) times of adult beetles feeding on 2nd instar and older stages of both scale species, (2) survival of beetle larvae fed single stages of each prey species, (3) scale cover morphology of both prey species, and (4) mandible morphology of adult *R. lophanthae* and *Chilochorus cacti* (L.). This latter coccinellid is a specialist predator of diaspidids but it is ineffective in suppressing California red scale in California citrus (Rosen and DeBach 1979).

Materials and Methods

Insect Cultures. Oleander scale, parthenogenetic strain (DeBach and White 1960), and California red scale were obtained from cultures maintained on lemons at the University of California, Riverside, using the rearing methods of Tashiro (1966). *R. lophanthae* was obtained from a stock culture maintained at the Riverside campus and supplemented with beetles collected from citrus at their Citrus Experimental Station. One subculture was maintained on *A. nerii*, whereas another was maintained on *A. aurantii*. Beetles were reared in 3-liter battery jars filled with lemons infested with either *A. nerii* or *A. aurantii* and covered with muslin cloth. The infested lemons were replaced weekly and the cultures were maintained in a temperature cabinet at $26.7 \pm 1^\circ\text{C}$, $65 \pm 5\%$ RH, and a photoperiod of 12:12 (L:D) h.

Food Preference Studies. Preference of *R. lophanthae* for *A. aurantii* or *A. nerii* was determined by exposing individual adults to a lemon infested with a mixture of equal numbers of the 2 prey species in the same stage. To ensure that similar sized prey of both species were present on a lemon, a fruit was infested twice, once with each species, and incubated until the desired scale age class was attained. Lemons infested with 2nd-instar scale were obtained by inoculation with scale crawlers on days 1 (*A. nerii*) and 6 (*A. aurantii*) and incubating the infested lemon for a total of 19 d. Lemons infested with 3rd-instar scale were obtained by inoculating with crawlers on days 1 (*A. nerii*) and 12 (*A. aurantii*) and incubating for a total of 33 d. Lemons infested with gravid females were obtained by inoculating with crawlers on days 1 and 12 and incubating the lemon for a total of 43 d. Lemons were incubated at $23.9 \pm 0.5^\circ\text{C}$, $55 \pm 5\%$ RH, and a photoperiod of 0:24 (L:D) h.

Standard arenas were constructed from 6-cm-diameter plastic vials. The top one-third of the vial had been cut and affixed to the fruit with modeling clay. A hole was cut in the snap-top lid and screen was glued over the hole before the lids were placed on the vials. An adult beetle was confined with prey in a standard arena and allowed to feed freely. The following 3 beetle preferences for the 2 diaspidids in 1 of 3 scale stages (= treatments) were

compared: (1) 2nd-instar *A. aurantii* versus 2nd-instar *A. nerii*, (2) 3rd-instar *A. aurantii* versus 3rd-instar *A. nerii*, and (3) mature female *A. aurantii* versus mature female *A. nerii*. Twenty-four adult beetles ≤ 1 -wk-old and reared on *A. aurantii* were divided into 3 groups of 8 replicates per treatment. Each beetle was starved for 24 h, placed in a standard arena, and allowed to feed 3 (treatment 1) or 4 h (treatments 2 and 3). The same protocol was used to determine the preference of adult beetles reared on *A. nerii* for the same 3 scale stages. Thus, 16 beetles were tested per treatment; half of which had been reared on *A. nerii* and half of which had been reared on *A. aurantii*.

Preference tests are only valid if a constant prey density is available to the predator (Cock 1970). To satisfy this condition, we provided an overabundance of each prey species in each replicate (≥ 40 prey per species per experiment) and exposed the scale to the predator for a short periods (3–4 h). Observations show that beetles rarely consumed more than five 3rd-instar or fifteen 2nd-instar scales over a 3- to 4-h period. To ensure the prey species were distributed evenly within an arena, scales were selectively removed as 2nd instars with a Pasteur pipette attached to a vacuum source. Although the absolute scale densities varied slightly on each experimental lemon, approximately equal proportions of each prey species were maintained.

A linear index of preference proposed by Strauss (1979) was used to compare beetle preference for a prey species ($L_i = r_i - P_i$) where r_i is the quotient of the number of *A. nerii* eaten divided by the total number of prey eaten per replicate and P_i is the proportion of *A. nerii* available in a replicate. L_i is the difference between 2 binomially distributed parameters ($r_i - P_i$) and is approximately normally distributed. Thus, this index can range from -1.0 to 1.0 , depending on the proportion of a given prey item (P_i) present in a replicate. In our experiments, both prey species occurred in approximately equal numbers; thus, P_i approximated 0.5 constraining L_i to values between -0.5 (complete avoidance) and $+0.5$ (complete preference). For each treatment, 2 mean L_i values were calculated: the summation of L_i values for the 8 beetles reared on *A. nerii* and the summation of L_i values for the 8 beetles reared on *A. aurantii*. We used a *t*-test (Strauss 1979) to compare whether the 2 L_i values differed significantly for beetles reared on the different prey species.

Handling Time. We determined the number of successful feeding attempts by adult *R. lophanthae* by continuously observing their feeding behavior on lemons infested with either gravid *A. nerii* or *A. aurantii*. The adult beetles used in the experiment were starved for 24 h before placing them unconfined on a scale-infested fruit at $23.9 \pm 0.5^\circ\text{C}$ (one beetle per fruit, $n = 10$). We recorded 5 behavioral events: (1) contacts, the number of scales physically contacted by the beetle; (2) palpations, the number of contacts that resulted in the

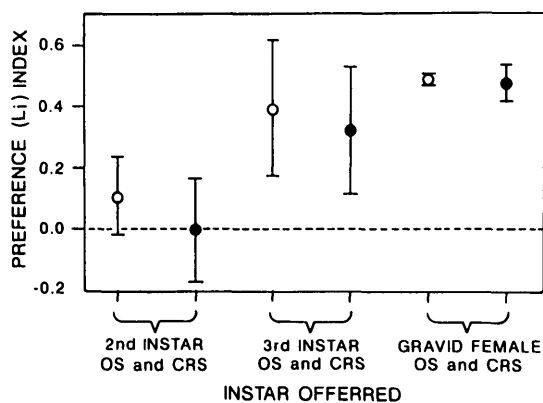


Fig. 1. Preference by *R. lophanthae* adults for 2nd-instar oleander scale (OS) versus 2nd-instar California red scale (CRS), early 3rd-instar *A. nerii* versus early 3rd-instar *A. aurantii*, and gravid *A. nerii* versus gravid *A. aurantii*. Dotted line indicates no preference, whereas positive values indicate a preference by *R. lophanthae* for *A. nerii* and negative values indicate a preference by *R. lophanthae* for *A. aurantii*. Open circles indicate *R. lophanthae* reared on *A. nerii* and closed circles indicate *R. lophanthae* reared on *A. aurantii* before testing. See text for the results of the statistical tests.

beetles drumming the scale cover with their maxillary palpi; (3) mandibular contacts, the number of drumming events that resulted in the beetle chewing the scale cover; (4) cover penetration, the number of chewing events that led to beetle penetration of the scale cover; and (5) scales consumed, the number of events in which the body beneath the cover was entirely consumed. An adult beetle reared on the prey species on which it was tested was observed until it was sated or had contacted a total of 15 scales, whichever came first. The results of these observations were presented as a flow chart, and the percentage of beetles progressing successfully from one event to the next was calculated by dividing the number of times the event was observed by the number of times the preceding event in the sequence had been completed. Differences in the percentage of beetles progressing to each event were compared for beetles feeding on the 2 prey species using chi-square.

We also measured the time it took each beetle to chew through the scale cover and consume the scale body of 2nd instar or older *A. nerii* or *A. aurantii*. We placed an adult beetle on a fruit infested with a single stage of the prey species on which the beetle had been reared and allowed the beetle to consume only one prey item. A stopwatch was used to measure the elapsed time between the time the beetle initiated mandibular activity on the scale cover and the time it walked away from the consumed scale. We included only those beetles that completely consumed a scale in the analysis. We compared the consumption times of the following 3 groups of beetles: (1) those feeding on 2nd-instar *A. nerii* versus those feeding on 2nd-

instar *A. aurantii*, (2) those feeding on early 3rd-instar *A. nerii* versus those feeding on virgin female *A. aurantii*, and (3) those feeding on gravid female *A. nerii* versus those feeding on gravid female *A. aurantii*. A Mann-Whitney *U* test was used to determine whether the handling times differed significantly between beetles feeding on the same stage of each prey species.

Larvae Survival Rates. Survival of *R. lophanthae* larvae from 1st instar until pupation was compared among beetle larvae offered the following: 1st-instar *A. nerii*, 1st-instar *A. aurantii*, 2nd-instar *A. nerii*, 2nd-instar *A. aurantii*, gravid *A. nerii*, gravid *A. aurantii*, a mixture of 2nd- and 3rd-instar female *A. nerii*, and a mixture of 2nd- and 3rd-instar *A. aurantii*. Lemons infested with 1st-instar scale were obtained by inoculating a fruit with *A. nerii* or *A. aurantii* crawlers and incubating the lemon for 13 and 7 d, respectively. Second-instar *A. nerii* and *A. aurantii* were obtained by incubating crawler-infested lemons for 20 and 15 d, respectively. Gravid females were obtained by incubating crawler-infested lemons for 40 and 30 d, respectively. Fruit with a mixture of 2nd- and 3rd-instar scales were inoculated twice (days 1 and 20 for *A. nerii*, days 1 and 12 for *A. aurantii*). These fruit were then incubated for a total of 39 d (*A. nerii*) or 27 d (*A. aurantii*). To ensure that *A. aurantii* females remained unmated, the scale-infested lemons were placed in plastic bags immediately after the male scales had been removed from the lemons with a dissecting needle 15 d after the 1st crawler inoculation. Lemons were incubated at $23.9 \pm 0.5^\circ\text{C}$, $55 \pm 5\%$ RH, and a photoperiod of 0:24 (L:D) h for *A. nerii* and $26.7 \pm 0.5^\circ\text{C}$, $60 \pm 5\%$ RH, and a photo period of 24:0 (L:D) h for *A. aurantii*. We used log linear models to test whether the survivorship of beetle larvae was independent of scale stage or species (Sokal and Rohlf 1981).

Each of the 8 treatments was replicated 8 times and each replicate consisted of 5 newly emerged, 1st-instar *R. lophanthae* larvae collected from a culture maintained on *A. nerii* ($n = 40$ larvae per treatment). A camel's-hair brush was used to place the neonate beetle larvae in a standard arena on an experimental lemon (above). Newly eclosed beetle larvae do not feed for the first 24 h and can be identified by their transparent head capsules and red eyes. The head capsules and eyes of the beetle larvae darken ≈ 2 h after eclosion. The neonate larvae were confined to a section of a scale infested lemon in a standard arena and were transferred daily to a fresh lemon infested with the appropriate scale species and stage. Larval mortality was assessed daily until pupation. Pupae were collected from the lemons within the arenas and held for emergence in 4-ml shell vials. The larvae were maintained in temperature cabinets at $26.7 \pm 1^\circ\text{C}$, $65 \pm 5\%$ RH, and a photoperiod of 12:12 (L:D) h. Cumulative survival of larvae (total surviving adults per original number of larvae per treatment)

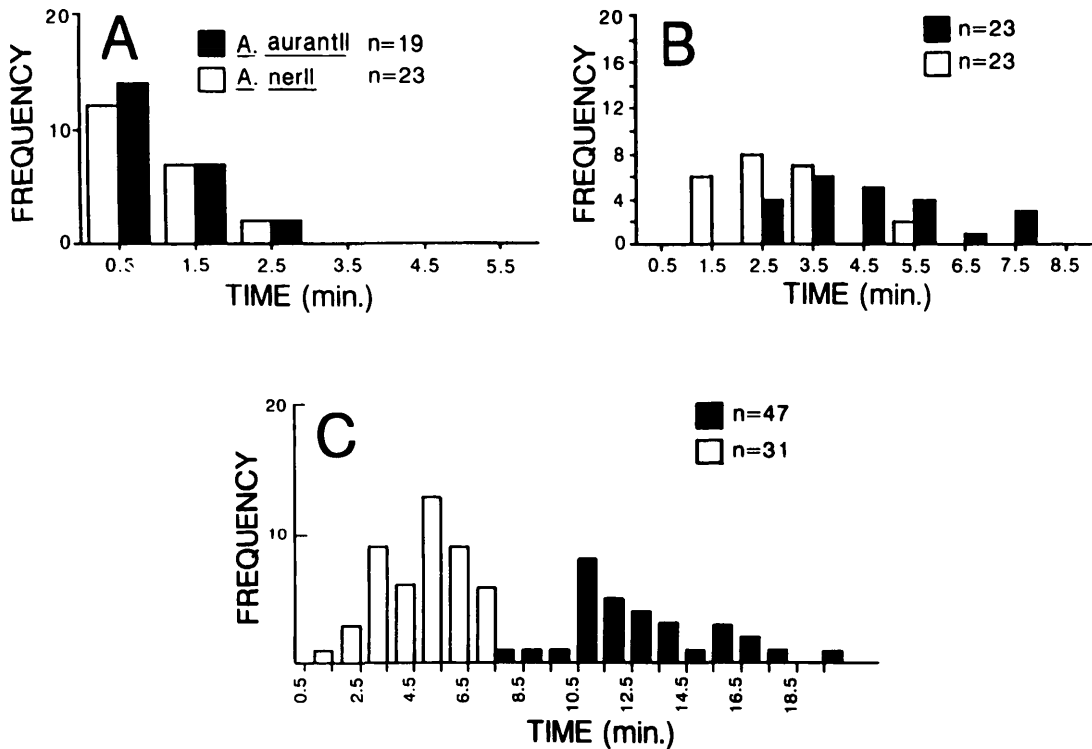


Fig. 2. Handling times of adult *R. lophanthae* when feeding on (A) 2nd-instar *A. nerii* versus 2nd-instar *A. aurantii*, (B) early 3rd-instar *A. nerii* versus early 3rd-instar *A. aurantii*, and (C) gravid *A. nerii* versus gravid *A. aurantii*.

was compared between scale species within each scale instar using chi-square.

Scanning Electron Microscopy. Scanning electron microscopy was used to examine the structure of intact scale covers of gravid *A. nerii* and *A. aurantii* and to view the feeding damage caused by adult *R. lophanthae* on the cover of each species. Mandibles of adult *R. lophanthae* and *C. cacti* were also examined to compare their morphology. Damaged and undamaged covers for each scale species were obtained by removing the covers from the appropriate host lemons and placing them in 2% osmium tetroxide for 48 h. The covers were then placed in a series of ethanol solutions for dehydration, critical-point dried, and mounted on alloy stubs with double-sided sticky tape. The mandibles were dissected from freshly killed beetles in a solution of 2% Triton-X and prepared as above. Scale covers and mandibles were coated with gold palladium and viewed using a JEOL-JSM 35c scanning electron microscope at 15 kV accelerating voltage.

Results

Preference Experiments. Adult beetles attacked 2nd and 3rd instar *A. nerii* and 2nd-instar male and female *A. aurantii* (Fig. 1). No preference for either scale species was detected when the beetles were offered a mixture of 2nd instars

of both species (*A. nerii*, $L_i = -0.003$, $t = 0.09$, $P > 0.10$; *A. aurantii*, $L_i = 0.108$, $t = 2.15$, $P > 0.01$). Furthermore, beetle preference was not influenced by the prey species on which it was reared ($t = 2.25$, $P > 0.10$). Observations indicate that 2nd-instar male *A. aurantii* was particularly attractive to the adult beetles as they were thinly covered and loosely attached to the fruit surface. (The *A. nerii* strain used in this study was parthenogenetic and thus, lacked males.) With increasing scale age (instar), however, *R. lophanthae* manifested an increasing preference for *A. nerii* (Fig. 1). Beetles reared on *A. nerii* and offered a choice between 3rd-instar *A. nerii* and 3rd-instar *A. aurantii* preferred *A. nerii* ($L_i = 0.393$, $t = 3.94$, $P < 0.01$). Although beetles reared on *A. aurantii* showed less preference for 3rd instar *A. nerii* ($L_i = 0.321$, $t = 2.87$, $P < 0.05$), this difference was not significant ($t = 0.18$, $P > 0.10$). The preference for *A. nerii* was even more pronounced when the beetles were offered gravid stages of both scale species (*A. nerii*-reared beetles, $L_i = 0.434$, $t = 31.21$, $P < 0.01$; *A. aurantii*-reared beetle, $L_i = 0.480$, $t = 30.36$, $P < 0.01$). Beetle preference was not influenced by the prey species on which it was reared ($t = 0.42$, $P > 0.10$).

Handling Times. As expected, the time required for an adult beetle to consume a prey item increased with scale instar (size) (Fig. 2). Less than 1 min was required for an adult to consume a 2nd-

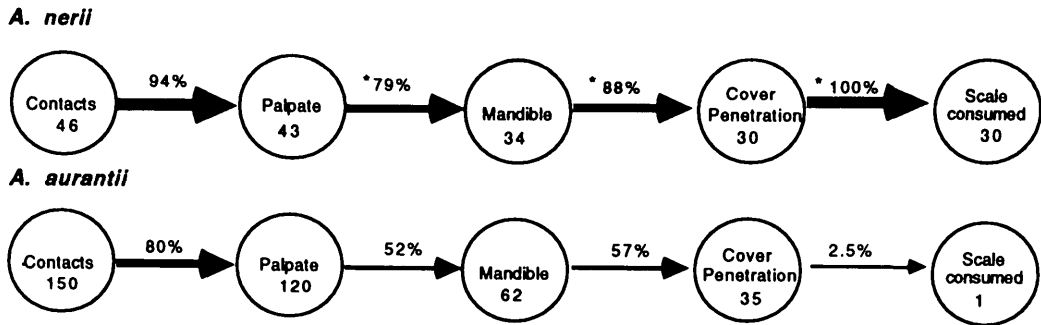


Fig. 3. Comparison of the percentage of adult *R. lophanthae* progressing from one event in the prey-feeding sequence to the next when feeding on gravid *A. nerii* versus gravid *A. aurantii*. An asterisk above the transition indicates a significant difference at the 5% level in the percentage of adult beetles progressing from the same feeding event in the *A. nerii* and *A. aurantii* sequences to the next event in the sequence.

instar *A. nerii* or *A. aurantii* (the instar prior to sexual dimorphism in *A. aurantii*) and the consumption times were similar for both prey species. However, consumption times differed significantly between prey species when the prey were 3rd instars. They were less for adults feeding on 3rd instar and gravid *A. nerii* (2.4 ± 1.87 min) than for those feeding on the same stages of *A. aurantii* (4.26 ± 1.06 min) (3rd instar: Mann-Whitney *U* test, $U = 416$, $P < 0.001$; gravid scales: Mann-Whitney *U* test, $U = 2600$, $P > 0.001$).

The differences in handling times among adult beetles fed gravid prey of each scale species was also reflected in the significant differences in the ratio of scale contacts to scales consumed (Fig. 3). Beetles contacting gravid *A. nerii* had little difficulty consuming them. However, those contacting gravid *A. aurantii* manifested a high failure rate. Normally, 2 gravid *A. nerii* sated an adult beetle and satiation usually occurred in <5 contacts with gravid scale. In contrast, beetles feeding on gravid *A. aurantii* often penetrated the scale cover but had difficulty penetrating the sclerotized scale body, at which point they often quit their feeding attempts on the scale and resumed searching.

The proportion of adult beetles progressing from one event to the next in the feeding sequence differed between beetles feeding on the gravid stage of the 2 prey species (Fig. 3). Those feeding on *A. nerii* consumed a significantly greater percentage of the scales they contacted when compared with beetles feeding on gravid *A. aurantii*. The proportion progressing from palpations to mandibular contacts ($\chi^2 = 8.72$, $df = 1$, $P < 0.01$); from mandibular contacts to cover penetrations ($\chi^2 = 8.74$, $df = 1$, $P < 0.01$); and from cover penetration to consumption ($\chi^2 = 107.13$, $df = 1$, $P < 0.001$) all differed significantly.

Larval Survival. More *R. lophanthae* neonate larvae completed development when they were reared on gravid *A. nerii* than on gravid *A. aurantii* (Table 1). One adult beetle was obtained from the 8 replicates ($n = 40$ neonate larvae) in which the larvae were fed gravid *A. aurantii*, whereas 32 adults were obtained from the 8 replicates ($n = 40$ neonate larvae) in which the larvae were fed gravid *A. nerii*. The proportion of beetle larvae surviving on an immature scale stage was independent of scale species (Table 1) even though the survivorship of beetle larvae increased with increasing age of the immature prey stage ($G_H = 78.57$, $df = 2$, $P < 0.001$). Mortality rates of beetle larvae fed only 1st instar were significantly higher than those fed 2nd-instar scales ($G = 27.82$, $df = 1$, $P < 0.001$). Most of this mortality occurred to the 4th-instar beetle larvae fed 1st-instar scale (50%), whereas larval survivorship remained high for the first 3 beetle larval instars. Fourth-instar beetle larvae were not observed to feed on 1st-instar scale nor were adult *R. lophanthae* observed to feed on scale crawlers or 1st-instar scale. Beetle larvae fed a mixture of 2nd and 3rd instars of either prey species survived the best of those fed immature scale ($G = 15.00$, $df = 1$, $P < 0.001$) and no deaths occurred to the larvae after they had molted to 2nd instars.

Mandibles. The outer surface of the adult mandible of *R. lophanthae* closely resembles that of

Table 1. Survival of *R. lophanthae* larvae from 1st instar to pupae when fed California red scale, *A. aurantii* or Oleander scale, *A. nerii* as single species, single stage or single species, mixed stages

Scale stage offered	Scale species offered	No. surviving larvae (n) [†]
1st instar	<i>A. nerii</i>	11(38)a
	<i>A. aurantii</i>	7(38)a
2nd instar	<i>A. nerii</i>	28(40)b
	<i>A. aurantii</i>	24(40)b
Late 2nd and early 3rd instar	<i>A. nerii</i>	37(40)c
	<i>A. aurantii</i>	35(40)c
Gravid females	<i>A. nerii</i>	32(40)c
	<i>A. aurantii</i>	1(40)a

Numbers followed by the same letter do not differ at the 5% level of significance. Criterion $G_{11, 0.05[7]} = 14.1$ (Sokal and Rohlf 1981).

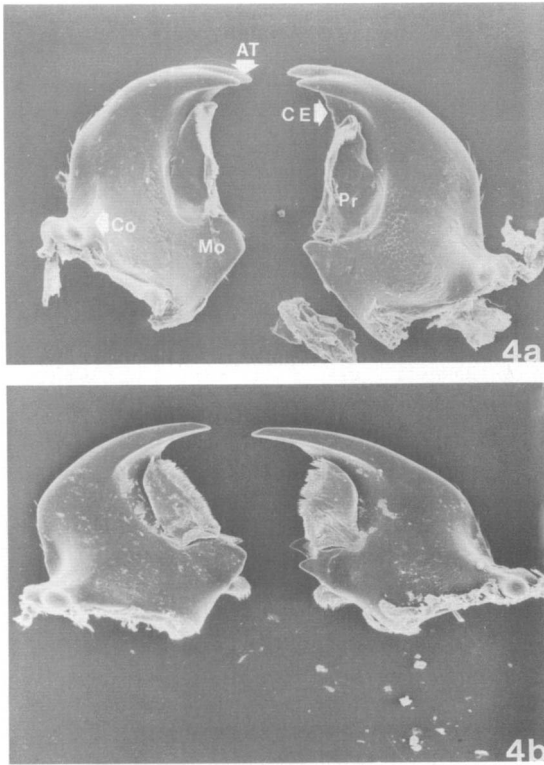


Fig. 4. Scanning electron micrograph of (a) adult *R. lophanthae* mandibles and (b) adult *C. cacti* mandibles. AT, apical tooth; CE, cutting edge; Pr, prostheca; Co, condyle; Mo, molar. Magnification 180 \times for *R. lophanthae* and 78 \times for *C. cacti*.

aphidophagous coccinellids (Hodek 1973) (Fig. 4A). It is simple, strongly curved, and concave at the base. The medial surface is sickle-shaped and forms an incisor at a bifid apex. The wide base of the mandible possesses acanthae and 2 condyles. The molar region consists of 1 tooth positioned on the medial surface. Ventrally, a membranous prostheca extends between the incisor and molar area and bears a continuous row of bristles, which are probably used for grooming or straining food (Hodek 1973). In contrast, the mandibles of *C. cacti* (Fig. 4B) demonstrate features common to this genus that are specialists on diaspidids. Their morphology has been described by Samways and Wilson (1988). These mandibles are more acutely angled and form a sharper incisor than those of *R. lophanthae*. The apex also has a single tooth which is used to pry scales from the substrate.

Scale Covers. In dorsal aspect, the covers of gravid *A. aurantii* are hard and circular (Fig. 5A). The central section is shown to be heavily sclerotized and composed of exuviae from the 1st and 2nd instars. The margin surrounding the centrally located exuviae consists of a substance that permeates the cover and appears to be the cementing material discharged from the Malpighian tubules by way of the anus (Stoetzel 1976) (Fig. 5B). The

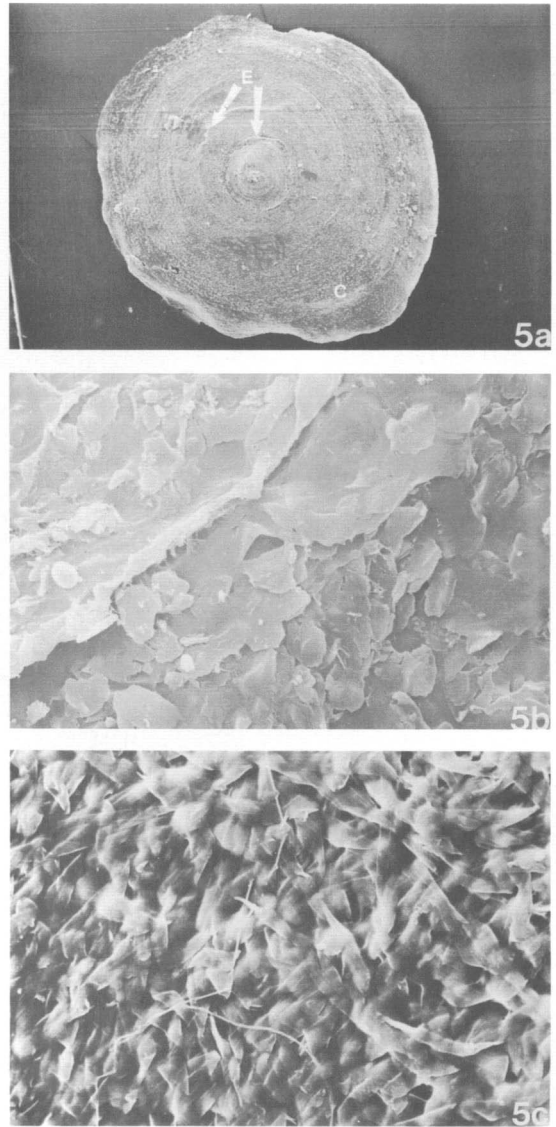


Fig. 5. Adult *A. aurantii* scale covers; (a) dorsal view; E, exuviae; C, cover. Magnification 36 \times , (b) dorsal view of cover distal of the exuviae; magnification 1,600 \times , and (c) ventral view of the scale cover distal of exuviae; magnification 1,200 \times .

cover margin is composed of a dense matrix of tightly interwoven filaments extruded from pores (macro- and microducts) located ventrally and dorsally on insect pygidium. The filaments are obscured by the cementing material dorsally but are apparent when the cover is viewed ventrally (Fig. 5C). In contrast to the cover of a gravid *A. aurantii*, that of a gravid *A. nerii* is thin and transparent (Fig. 6). It is also apparently composed of loosely interwoven filaments arising from both micro- and macroducts. However, the exuviae are only lightly sclerotized and the cementing material present in *A. aurantii* covers is greatly reduced or lacking in those of *A. nerii*.

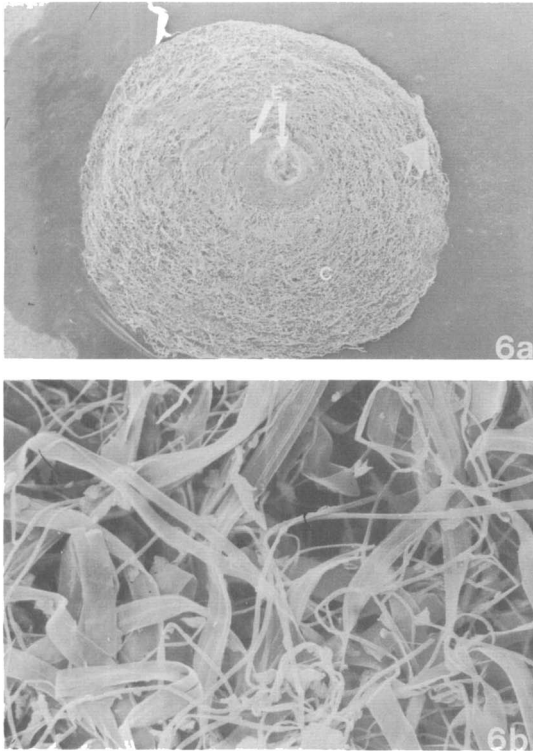


Fig. 6. Adult *A. nerii* scale cover (a) dorsal view of the cover; E, exuviae; C, cover, magnification 44x, and (b) dorsal view of the scale cover distal to the exuviae, magnification 1,600x.

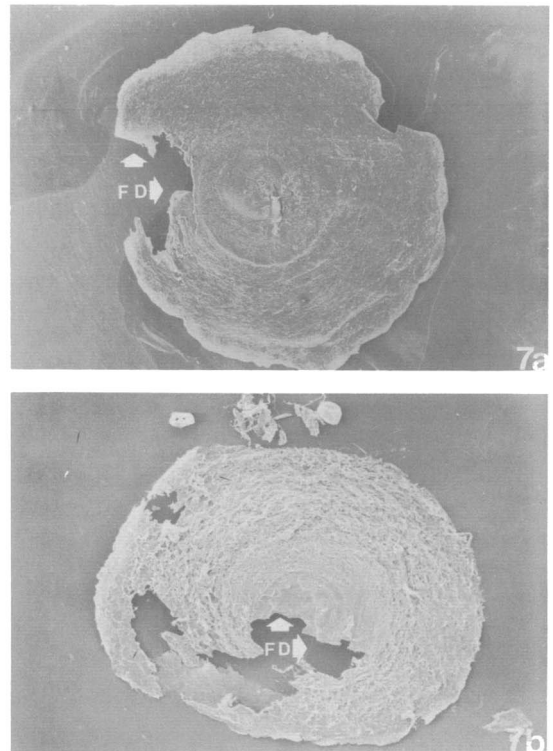


Fig. 7. Feeding damage (FD) by *R. lophanthae* to (a) an *A. aurantii* scale cover, dorsal view, magnification 40x, and (b) to an *A. nerii* scale cover, dorsal view, magnification 44x.

The differences in the feeding damage observed on the scale covers of each prey species appears to be correlated with differences in scale cover morphology. Feeding damage by adult *R. lophanthae* on a gravid *A. aurantii* cover is characteristically limited to a small area on the cover margin peripheral to the exuviae (Fig. 7A). The feeding scars suggest that margin texture is very dense and brittle and appears to have been chipped away when fed on by the beetle. Typically, the central section containing the exuviae remains undamaged. Behavioral observations show that larval and adult beetles cannot penetrate this central section because their mandibles slide off when they attempt to bite. Moreover, once the beetles have penetrated the cover margin they are confronted with a 2nd barrier; the sclerotized scale body which is strongly attached to the substrate. *R. lophanthae* is largely unsuccessful in feeding on this scale stage. In contrast, the entire cover of a gravid *A. nerii* can sustain damage and is easily shredded, torn, and consumed by the predator (Fig. 7B). It is not unusual for beetles to consume large portions of the cover or even the entire cover. Moreover, once having penetrated the cover, the gravid body of *A. nerii* beneath is soft, unsclerotized, and unattached to the substrate.

Discussion

Rhyzobius lophanthae develops and reproduces readily on 2nd-instar male and female, and 3rd-instar *A. aurantii* and on 2nd-instar and older *A. nerii*. Thus, both scale species can serve as prey for the predator (sensu Hodek 1973). But these prey species and stages are not of equal value. Morphological features of both the predator and prey influence the ability of *R. lophanthae* to exploit them and the prey stages differ in the amount of nutrition they offer. Morphologically, the mandibles of *R. lophanthae* are similar to those of the aphid-feeding coccinellids (Hodek 1973) and appear ill suited to prey on gravid *A. aurantii* or other scale species with hardened covers. The adult beetle requires long periods to penetrate the hard cover. Once having penetrated the cover, it is then faced with the sclerotized scale body, which further impedes its feeding. However, *R. lophanthae* mandibles appear capable of handling the smaller, softer covers of immature stages of both scale species and the covers of the gravid and parturient stages of *A. nerii* lacking cementing material.

In contrast, the mandibles of the diaspidid-feeding *Chilocorus* are highly modified and unique to the genus. They are acutely angled and possess a single tooth at their apex, which can be inserted

between the scale and the substrate to pry the scale loose (Hodek 1973, Samways and Wilson 1988). When feeding on diaspidids they frequently straddle the scale while maintaining contact with the substrate with their mid- and hindlegs. Their forelegs are splayed laterally against the rim of the scale while the tooth of the mandible is inserted between the substrate and scale. The beetle then pushes its body away from the substrate and uses the mandible to pry the scale from the substrate, flipping the scale upside down in the process. This behavior exposes the softer ventral surface of scale body which is easily eaten (Samways and Wilson 1988). Although *R. lophanthae* attempts a similar feeding tactic with gravid *A. aurantii*, its smaller size and generalized mandibles make it much less successful than *Chilocorus*. Furthermore, because of their large size, adult *Chilocorus* can easily chew through the covers of gravid *A. aurantii* (Samways and Wilson 1988).

Beardsley and Gonzalez (1975) and Stoetzel (1976) hypothesized that armored scale covers serve as a defense against natural enemies. Our results suggest this is true for only some species of armored scales. Although both *A. nerii* and *A. aurantii* construct a protective covering composed of filaments extruded from the pygidium, the cover of *A. nerii* is soft and easily penetrated by the coccinellid predators. In contrast, the hardened cover of the gravid and parturient *A. aurantii* offers some protection from generalized predators by forming a physical barrier to beetle feeding. Cover hardness appears to result from enzymatic polymerization of the filaments in the cover (Ebstein and Gerson 1970; Pesson and Foldi 1978; Foldi 1983, 1990) and from the incorporation of the exuviae of the 1st and 2nd molt into the scale cover.

Physical defense offered by the hardened cover of *A. aurantii* is complemented by the sclerotized integument of the gravid and parturient scale body and by a ventral sheath beneath the body that strongly attaches the body to the substrate (Dickson 1951). The sclerotized body provides a 2nd, hardened, dorsal barrier to beetle feeding. Even so, *R. lophanthae* can feed on a gravid *A. aurantii* either by chewing through the cover and penetrating the sclerotized integument or, alternatively, by separating the scale from its substrate and feeding on the softer ventral surface of the body. Either of these processes, however, is difficult and time consuming as suggested by the adult consumption times (Fig. 3) and failure rates (Fig. 2). Furthermore, *R. lophanthae* larvae usually failed to survive when offered only gravid *A. aurantii* as food. In contrast, gravid *A. nerii* develop neither a hardened cover or sclerotized body and are substantially more vulnerable to predation by *R. lophanthae*. *R. lophanthae* larvae readily develop on this species. Moreover, adult female beetles reared on and fed *A. nerii* laid significantly more eggs (mean = 136.2 ± 18.6 SD, $n = 13$) than did those reared and fed *A. aurantii* (mean = 37.3 ± 19.3 SD, $n =$

15) ($t = 2.54$, $P < 0.05$). All of these elements suggest that *A. nerii* is a substantially more valuable resource for *R. lophanthae*.

Differences in predation success and consumption times should be reflected in predator preference for prey stages and species based on the economic principal that prey stage or species yielding the most energy gain per unit energy expended should be preferred (Stephens and Krebs 1986, Krebs and Davies 1991). This appears to be the case with *R. lophanthae*. When offered a choice between either 3rd-instar or gravid *A. nerii* and *A. aurantii* in either a single-stage, mixed-species, or a mixed-stage, mixed-species experiment, the predator preferred 3rd-instar and gravid *A. nerii* (Fig. 1). If predator consumption time for these stages is an index of its energy expenditure when consuming them and both scale species are equally nutritious per unit body weight, then the beetle expends more energy obtaining a unit of *A. aurantii* than a unit of *A. nerii* (Fig. 2). Thus, prey preference by *R. lophanthae* is consistent with expectations.

Anecdotally, adult *R. lophanthae* showed little initial preference for the gravid stage of either species when they first encountered these stages in an arena containing the mixture of gravid stages of the 2 species. They only began to discriminate against *A. aurantii* in favor of *A. nerii* after they repeatedly failed to penetrate the integument of *A. aurantii*.

Rhyzobius lophanthae was unable to suppress *A. aurantii* populations successfully in California following its introduction in 1898 (Rosen and DeBach 1979). Several factors probably combined with the restricted vulnerability of *A. aurantii* to influence *R. lophanthae* efficacy in suppressing populations of this scale in the field. Hagen (1974) suggested that successful biological control by a coccinellid is most likely to occur when the predator manifests the following 7 attributes: (1) has the same climatic tolerance as its prey species, (2) is prey specific, (3) utilizes all stages of a prey species, (4) is highly vagile, (5) is synchronized with a prey species, (6) has a long reproductive life with high reproductive potential, and (7) lacks natural enemies. With respect to *A. aurantii*, *R. lophanthae* possess many of these attributes. It survives in the same climatic regions as *A. aurantii* (Gordon 1985), has no recorded natural enemies, colonizes and disperses rapidly when introduced, and reproduces in large numbers (Rubstov 1952, Greathead 1973). However, it is polyphagous, feeding on a number of diaspidid species (Gordon 1985), its life cycle is not well synchronized to that of *A. aurantii*, and it does not feed readily on all stages of *A. aurantii*. Thus, the dynamics of the prey population, that is, the proportion of prey life span in which it is vulnerable coupled with the age structure of the scale population, influence the ability of *R. lophanthae* to regulate the scale population. For example, although the duration of 2nd-instar male and female, and 3rd-instar *A. aurantii* in the

field varies depending on temperature, these 2 stages represent only 25% of the life span of *A. aurantii*, whereas the relatively immune gravid and parturient stage represent 67% of the scale life span (Yu and Luck 1988). The adult beetles do not utilize 1st-instar scales. Thus, only 2nd- and 3rd-instar scales are a resource for adult *R. lophanthae* and these stages must be present in a population in sufficient numbers to entice the predator to feed and reproduce. Even if the beetle reproduces, 2nd- and early 3rd-instar scale are important to larval survival and development. Young beetle larvae (1st, 2nd, and 3rd instars) can survive on 1st-instar *A. aurantii*, but 4th-instar larvae require the older scale instars if they are to survive in substantial numbers. Moreover, few larvae are able to survive and develop on gravid or parturient scales, and those that do are small and less fecund. *Chilocorus* larvae are also unable to feed on mature scale stages with hard covers (Drea 1978), probably because of the differences in the morphology of their mandibles when compared with those of the adult (Rees et al. 1994). Additionally, the time required for a beetle larva to develop to pupation exceeds the development time for a cohort of 2nd- and 3rd-instar scale. Thus, overlapping stages of *A. aurantii* (2nd and early 3rd instars) in sufficient densities are essential if predator larvae are to mature but this density appears to exceed the economic threshold for the scale (Rosen and DeBach 1979). These conditions make the biological control of *A. aurantii* by *R. lophanthae* unlikely when it is the sole agent present. The predator may be an important adjunct to the more specific natural enemies of scale, for example, *Aphytis melinus*, because the beetle feeds on the small scale patches on leaves and fruit missed by *A. melinus* and on the scale population inhabiting the scaffolding branches and tree trunk, a site in which *A. melinus* is of limited effectiveness (Walde et al. 1989, Yu et al. 1990; R.F.L. and L. Forster, unpublished data).

In contrast, *A. nerii* is vulnerable to predation throughout its life span. Moreover, the older stages of this scale, because of their size, appear to offer more resources per scale individual than *A. aurantii*. Pizzamiglio (1985) reports that *R. lophanthae* is the principal natural enemy of *A. nerii* on California bay, *Umbellularia californica* (Hopk. and Arn.), in California and regulates the scale species at very low densities. Thus, the ability of *R. lophanthae* to control a scale species appears to depend on a combination of predator and prey morphology and the age structure dynamics of the prey population. These results support the Clausen (1940) hypothesis, that is, that diaspidid species with soft covers throughout their life span are more likely to be controlled by coccinellid predators.

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