**Israel Journal of Entomology**
**Vol. XXV-XXVI (1991-1992) pp.57-65**

# ENCAPSULATION OF EGGS OF TWO SPECIES OF *ENCYRTUS* (HYMENOPTERA : ENCYRTIDAE) BY SOFT SCALES (HOMOPTERA : COCCIDAE) IN SIX PARASITOID-HOST INTERACTIONS*

D. BLUMBERG AND S. GOLDENBERG
*Department of Entomology, Institute of Plant Protection,*
*Agricultural Research Organization, The Volcani Center, Bet Dagan 50250, Israel*

**ABSTRACT**

The encapsulation of eggs of *Encyrtus infelix* (Embleton) by the hemispherical scale, *Saissetia coffeae* (Walker), the pyriform scale, *Protopulvinaria pyriformis* (Cockerell), the brown soft scale**,** *Coccus hesperidum* L., the nigra scale, *Parasaissetia nigra* (Nietner), and *Pulvinaria urbicola* Cockerell, as well as the encapsulation of eggs of *E. lecaniorum* (Mayr) by C**.** *hesperidum***,** were determined under controlled laboratory conditions. The rates of efficient encapsulation (percent scales wherein encapsulation completely prevented parasitoid development) of *E. infelix* eggs by *S. coffeae* at 28°C were low (2-8%), being almost as frequent in Dec. 1987 as in Sept. 1989 and in Jan. 1991. At32°C, efficient encapsulation in scales parasitized in Jan. 1991 was significantly lower (34%) than in scales parasitized in Jan. 1988 (100%). Encapsulation of *E. lecaniorum* eggs by C. *hesperidum* at 28°C was significantly lower in young female scales than in mature scales (18.4% vs. 83.5% efficient encapsulation). At 32°C almost all *E. lecaniorum* eggs became encapsulated by mature females of *C. hesperidum.*

Superparasitism by *E. lecaniorum* in *C. hesperidum* at 28°C, occurring in 84% of the parasitized young female scales, was advantageous to the parasitoid, since it led to significantly more surviving progeny than solitary parasitism. Oviposition by *E. infelix* in *P. pyriformis* resulted in 95-100% encapsulation of parasitoid eggs, therefore preventing almost any parasitoid development. Exposure of P. *pyriformis* to 40°C for 24 h prior to parasitism by *E. infelix* significantly reduced the incidence of encapsulation and successful parasitoid development was recorded in approximately 70% of the parasitized scales. Development of E. *infelix* in *C. hesperidum, P. nigra,* and P. *urbicola* was entirely prevented due to a complete parasitoid egg encapsulation.

***KEY WORDS:*** *Encyrtus infelix, Encyrtus lecaniorum, Saissetia coffeae, Saissetia oleae, Coccus hesperidum, Parasaissetia nigra, Pulvinaria urbicola, Protopulvinaria pyriformis, soft scales, parasitoid egg encapsulation.*

## INTRODUCTION

Encapsulation as a common defense mechanism of insect hosts against internal parasitoids is considered an important parameter of host suitability (Bess, 1939; Salt, 1963; Bartlett and Ball, 1966; Blumberg, 1977; Vinson and Iwantsch, 1980; Dijkerman, 1990). High frequencies of encapsulation may adversely affect parasitoid efficacy in the field (Muldrew, 1953; Brewer, 1971; Blumberg, 1991) and likewise may cause difficulties in mass rearing of parasitoids (Reed et al., 1968; Blumberg, 1977).

*Contribution from the Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel. No. 3291-E 1991.

Species of the genus *Encyrtus* Latreille (Hymenoptera : Encyrtidae) are cosmopolitan primary parasitoids of soft scales (Homoptera : Coccidae) (Nikolskaja, 1952; Peck, 1963). *Encyrtus infelix* (Embleton) is a parasitoid of the hemispherical scale, *Saissetia coffeae* (Walker) (Thorpe, 1936; Maple, 1947). Thorpe (1936) described the life history of *E. infelix* and especially its respiratory relationships with *S. coffeae*, which are of an extraordinary character. The parasitoid is considered an important biological control agent of *S. coffeae* in California (Bartlett, 1978) and has been used in France for scale control in glasshouses (Copland and Ibrahim, 1985). The occurrence of *E. infelix* in Israel was recorded, probably for the first time, in June 1987, when several parasitoid adults emerged from *S. coffeae* collected by Mr. A. Rubin (Biological Control Laboratory, Givat Shmuel, Israel) on *Pseuderanthemum* sp. (Araliaceae) in a glasshouse in Jerusalem.

*Encyrtus lecaniorum* (Mayr) is a parasitoid of the brown soft scale, *Coccus hesperidum* L. It is widespread in South Africa, occurring also in many other parts of the world (Annecke, 1964; Rosen, 1967; Prinsloo, 1984). In South Africa it is regarded as an important natural enemy of that host (Annecke, 1964). Rivnay (1944) and Bodenheimer (1951) recorded *E. lecaniorum* as the dominant parasitoid of *C. hesperidum* in Palestine, whereas Rosen (1967) found it to be very rare and of no economic value along the Coastal Plain of Israel. Both *E. infelix* and *E. lecaniorum* develop solitarily, mainly in the young female stage of their host. Males of both species are scarce and the females are capable of continuous parthenogenetic development. *S. coffeae* and *C. hesperidum* are polyphagous cosmopolitan species. In Israel, the first coccid is a common pest of olives and ornamentals (Avidov and Harpaz, 1969; Rosen et al., 1971), while the second is prevalent in citrus groves and on ornamentals (Avidov and Harpaz, 1969).

In addition to *S. coffeae* and *C. hesperidum*, four other coccids were propagated in our insectary for evaluation of their possible use as alternative hosts for various parasitoids of soft scales. These coccids were: (i) the Mediterranean black scale, *Saissetia oleae* (Olivier); (ii) the pyriform scale, *Protopulvinaria pyriformis* (Cockerell); (iii) the nigra scale, *Parasaissetia nigra* (Nietner); and (iv) *Pulvinaria urbicola* Cockerell. Preliminary observations in the insectary cultures of the two *Encyrtus* species revealed some parasitoid egg encapsulation in both *S. coffeae* and *C. hesperidum*.

This paper reports on the encapsulation response of *S. coffeae* and *C. hesperidum* to parasitism by their parasitoids, *E. infelix* and *E. lecaniorum*, respectively, under different rearing conditions. The suitability of *S. oleae*, *P. pyriformis*, *P. nigra*, and *P. urbicola* as alternative hosts for the two *Encyrtus* species, as regards host ovipositional attraction and parasitoid egg encapsulation, was also studied.

## MATERIALS AND METHODS

Detached potato sprouts were used for propagating *S. coffeae*, *S. oleae*, and *P. urbicola* (Blumberg and Swirski, 1977) and butternut squash (*Cucurbita moschata*) was used for rearing *C. hesperidum* and *P. nigra*. *Protopulvinaria pyriformis* was propagated on saplings of *Hedera helix* and *Fatsia japonica* (Araliaceae). Insectary cultures of *E. infelix* and *E. lecaniorum* were established on *S. coffeae* and *C. hesperidum*, respectively. The host and parasitoid cultures were maintained at 24 ± 2°C and 60–70% R.H. in plastic rearing cages (28.0 × 17.5 × 12.5 cm). For each experiment of parasitoid–host interaction, female scales were exposed to oviposition by 50–100 adult parasitoids in closed and ventilated plastic cages (10.5 × 10.5 × 14.0 cm), at constant temperatures (28 or 32°C) for 24 h. Preliminary observations had shown that this duration of host exposure brought about a high parasitism rate, but also left many unparasitized scales. About 40–120 parasitized scales, in five to nine replicates, were examined in each experiment. Scales containing encapsulated eggs of either parasitoid species could easily be recognized even without dissection as soon as 24 h after parasitism. This was due to the melanized capsule which surrounded the entire parasitoid egg and was clearly seen throughout the host body dorsum. However, to determine the presence of parasitoid larva(e) within the host body at early stages of parasitoid development,

scales were dissected 8–12 days after removal of adult parasitoids. The incidence of encapsulation was assessed as (i) percentage of encapsulated eggs, and (ii) percentage of parasitized scales wherein encapsulation completely prevented parasitoid development, which reflects the rate of efficient encapsulation (Blumberg, 1991). To examine whether the continuous exposure of *E. infelix* to *S. coffeae* under insectary conditions could affect the host's encapsulation ability, encapsulation frequencies in this parasitoid–host interaction were determined (i) at 28°C, in three different periods with about 2-year intervals from the establishment of the insectary culture in July 1987; and (ii) at 32°C, in two periods at a 3-year interval from the establishment.

To examine the suitability of *P. pyriformis* as a host for larval development of *E. infelix* it was first necessary to reduce intentionally the incidence of parasitoid encapsulation by the host. This was achieved by subjecting scale-infested saplings of *H. helix* and *F. japonica* to 40°C for 24 h prior to the exposure of the scales for parasitoid oviposition (Blumberg, 1976).

Data (percentages) were transformed into arcsine values and subjected to ANOVA. Significance between means was determined using Duncan's Multiple Range Test (1955).

## RESULTS AND DISCUSSION

### I. Ovipositional attractiveness

*Encyrtus infelix* did not refrain from ovipositing in young and preovipositing females of *S. coffeae*, *C. hesperidum*, *P. pyriformis*, *P. nigra*, and *P urbicola*, but was not attracted for oviposition by *S. oleae*. *Encyrtus lecaniorum* oviposited only in *C. hesperidum* and not in any of the five other above-mentioned coccids. Thus, as regard host acceptance, *E. lecaniorum* may be considered more specific than *E. infelix*.

### II. Encapsulation of *E. infelix* eggs by *S. coffeae*

Table 1 shows the incidences of encapsulation of *E. infelix* eggs by *S. coffeae* as determined at 28° and 32°C, at various periods (5 to 42 months) after the establishment of the parasitoid culture in our insectary. At 28°C, encapsulation rates (both percentages of eggs encapsulated and efficient encapsulation) were relatively low and prevention of parasitoid development due to encapsulation occurred only in about 2–8% of the overall parasitized scales dissected. No significant differences were recorded in the percentage of efficient encapsulation measured at each of the three dates. However, the percentage of eggs encapsulated in Jan. 1991 was significantly lower than in Dec. 1987 or in Sept. 1989. At 32°C, encapsulation in scales parasitized in Jan. 1988 included all parasitoid eggs, thereby preventing any parasitoid development. Three years later, encapsulation rates at 32°C were significantly lower and, as a result, developing parasitoid larvae were observed in most (80%) of the parasitized scales at the time they were dissected. However, none of these larvae was able to complete its development at that temperature, which probably was detrimental to both the parasitoid and the host. It is suggested that the successive rearing of approximately 40 generations of *E. infelix* on *S. coffeae* under controlled insectary conditions enhanced and improved the adaptability of the parasitoid to its host. This enhanced adaptability, manifested in a reduction of the host's encapsulation ability, was more pronounced at 32 than at 28°C, probably because of the initial rates of encapsulation, which were maximal (100%) at 32°C.

In this regard Messenger and van den Bosch (1971) demonstrated that in the interaction between the ichneumonid parasitoid *Bathyplectes curculionis* (Thomson) and its host, the alfalfa weevil, *Hypera brunneipennis* (Boheman), the host's encapsulation capacity started at a high level and gradually decreased as the parasitoid progressively adapted to its host.

Four conditions of parasitoid development and encapsulation were detected at the time of dissection in parasitized scales wherein encapsulation did not prevent parasitoid development (Table 2). At either 28 or 32°C most of the scales (84% and 72%, respectively) contained a solitary free developing parasitoid larva. Some parasitized scales (7–12%) contained larvae that were

TABLE 1
Encapsulation of *Encyrtus infelix* eggs by *Saissetia coffeae*[1]

| Rearing temperature (°C) | Date | Parasitoid eggs: Total number observed | Parasitoid eggs: Encapsulated n | Parasitoid eggs: Encapsulated Mean (%) ± S.D. | Parasitized scales: Total number dissected | Parasitized scales: With encapsulated egg(s) only[2] n | Parasitized scales: With encapsulated egg(s) only[2] Mean (%) ± S.D. |
|---|---|---|---|---|---|---|---|
| 28 | Dec. 1987 | 406 | 65 | 15.7 ± 6.8a | 352 | 29 | 7.8 ± 5.6a |
| | Sept. 1989 | 429 | 75 | 15.5 ± 9.5a | 411 | 27 | 6.3 ± 5.2a |
| | Jan. 1991 | 297 | 21 | 6.3 ± 4.3b | 287 | 3 | 2.0 ± 2.0a |
| 32 | Jan. 1988 | 212 | 212 | 100a | 203 | 203 | 100a |
| | Jan. 1991 | 596 | 226 | 34.1 ± 2.0b | 460 | 95 | 20.6 ± 15.4b |

[1]Within columns, means followed by the same letter do not differ significantly ($P = 0.05$), Duncan's Multiple Range Test.
[2]Efficient encapsulation.

TABLE 2
Conditions of parasitoid development and encapsulation in young female scales, in two parasitoid–host interactions wherein parasitoid development was not prevented by encapsulation

| Parasitized scales containing: | Rearing temp. (°C) | Number (n) and percent of scales in parasitoid–host interaction: *E. infelix–S. coffeae* n | *E. infelix–S. coffeae* % | *E. lecaniorum –C. hesperidum* n | *E. lecaniorum –C. hesperidum* % |
|---|---|---|---|---|---|
| A free developing larva | 28 | 833 | 83.9 | 1 | 0.8 |
| | 32 | 262 | 71.8 | | |
| A developing larva attached to an egg capsule | 28 | 69 | 6.9 | 0 | 0 |
| | 32 | 45 | 12.3 | – | – |
| A free developing larva and 1–3 encapsulated eggs | 28 | 91 | 9.2 | 117 | 99.2 |
| | 32 | 43 | 11.8 | | |
| A developing larva attached to an egg capsule and 1–3 encapsulated eggs | 28 | 0 | 0 | 0 | 0 |
| | 32 | 15 | 4.1 | – | – |

attached to egg capsules. The occurrence of such attached larvae in some parasitized scales indicates that even if a capsule is formed around a parasitoid egg, it is not always sufficiently effective in preventing parasitoid egg hatch and development.

Egg capsules from which parasitoid larvae escaped and developed normally were observed in *S. coffeae* parasitized by the encyrtid *Metaphycus* aff. *stanleyi* (Compere) (=*M. swirskii* Annecke and Mynhardt) (Blumberg, 1977). Table 4 shows that out of 1051 parasitized young female scales dissected only 9.7% were superparasitized. The incidences of parasitized scales containing a developing parasitoid larva and of those containing only encapsulated egg(s), were as frequent in

solitary parasitized scales as in superparasitized ones. The presence of multiple eggs of *E. infelix* in *S. coffeae* therefore did not affect the incidence of parasitoid encapsulation.

### III. Encapsulation of *E. lecaniorum* eggs by *C. hesperidum*

Table 3 shows that at 28 and 32°C almost all parasitized scales contained at least one encapsulated egg (together with or without a developing parasitoid). At 28°C approximately 65% of the total parasitoid eggs became encapsulated in young female scales, but only in 18.4% of the overall parasitized scales of that age did encapsulation include all parasitoid eggs, thereby preventing any parasitoid development. At 32°C, parasitoid development was prevented in almost all (99%) of the parasitized mature (preovipositing and ovipositing) female scales due to encapsulation, and this was significantly higher than at 28°C. Reed et al. (1968) also reported on the total egg encapsulation of *E. lecaniorum* by *C. hesperidum* when the parasitized host was held at 32.2°C. At 28°C, encapsulation of *E. lecaniorum* eggs by mature females of *C. hesperidum* was significantly more frequent than by young females of the host (Table 3), indicating that older hosts were capable of encapsulating parasitoid eggs more efficiently than younger ones. The combined effects of host age and rearing temperature on increasing the incidence of parasitoid encapsulation were likewise demonstrated in the interactions between (a) *M. swirskii* and *S. oleae* (Blumberg, 1982), (b) *M. swirskii* and *S. coffeae* (Blumberg, 1988), and (c) *M. stanleyi and C. hesperidum* (Blumberg and DeBach, 1981). No larvae of *E. lecaniorum* attached to egg capsules (as occurred with *E. infelix* in *S. coffeae*) were detected in *C. hesperidum.* Most of the parasitized young female scales (99.2%) wherein parasitoid development was not prevented by encapsulation contained a developing parasitoid together with one to three encapsulated eggs (Table 2).

TABLE 3
Encapsulation of *Encyrtus lecaniorum* eggs by *Coccus hesperidum*[1]

| Rearing temperature (°C) | Physiological age of female scales | Parasitoid eggs: Total observed | Parasitoid eggs: Encapsulated n | Parasitoid eggs: Encapsulated Mean (%) ± S.D. | Parasitized scales: Total number dissected | Parasitized scales: With at least one encapsulated egg n | Parasitized scales: With at least one encapsulated egg Mean (%) | Parasitized scales: With encapsulated egg(s) only[2] n | Parasitized scales: With encapsulated egg(s) only[2] Mean (%) ± S.D. |
|---|---|---|---|---|---|---|---|---|---|
| 28 | Young | 339 | 221 | 64.8 ± 6.9a | 147 | 146 | 99.6a | 29 | 18.4 ± 18.7a |
| | Mature[3] | 500 | 463 | 92.4 ± 4.8b | 229 | 224 | 97.6a | 191 | 83.5 ± 12.5b |
| 32 | Mature[3] | – | – | – | 143 | 140 | 98.8a | 140 | 98.8 ± 2.1c |

[1]Within columns, means followed by the same letter do not differ significantly ($P = 0.05$), Duncan's Multiple Range Test.
[2]Efficient encapsulation.
[3]Pre-reproducing and/or reproducing females.

Table 4 shows that out of 147 parasitized young female scales dissected, approximately 84% were superparasitized, containing two to seven parasitoid eggs per scale. The incidence of scales with a developing parasitoid larva in superparasitized scales was 95.1%, as compared with only 4.2% in solitary parasitized ones. This reduction in parasitoid encapsulation in superparasitized scales is probably an adaptation to the higher rates of encapsulation encountered by the solitary eggs of *E. lecaniorum.* Similarly, Puttler (1959) found 92% encapsulation of the ichneumonid *Hyposoter exiguae* (Viereck) in larvae of the beet armyworm *Laphygma exiqua* (Hubner) which

TABLE 4
Encapsulation of solitary and multiple eggs by young female scales in two parasitoid–host interactions at 28°C

| Parasitoid–host interaction | Number of parasitoid eggs/scale | Parasitized scales dissected: With a developing parasitoid larva n | With a developing parasitoid larva % | With encapsulated egg(s) only n | With encapsulated egg(s) only % | Total | Percent superparasitism |
|---|---|---|---|---|---|---|---|
| *E. infelix* – | 1 | 897 | 94.5 | 52 | 5.5 | 949 | 9.7 |
| *S. coffeae* | 2–4 | 95 | 93.1 | 7 | 6.7 | 1051 | |
| *E. lecaniorum* – | 1 | 1 | 4.2 | 23 | 95.8 | 24 | 83.7 |
| *C. hesperidum* | 2–7 | 117 | 95.1 | 6 | 4.9 | 123 | |

contained a single parasitoid egg as compared with 3.3% encapsulation in superparasitized individuals. Likewise, Blumberg and Luck (1990) have demonstrated that multiple eggs of the California strain of the encyrtid parasitoid *Comperiella bifasciata* (Howard) were less likely to be encapsulated in the California red scale, *Aonidiella aurantii* (Maskell), than solitary eggs of the parasitoid. Superparasitism, as presently found in the interaction between *E. lecaniorum* and *C. hesperidum*, leads to more surviving progeny than solitary parasitism and is therefore advantageous to the parasitoid (Streams, 1971; van Alphen and Visser, 1990; Giordanengo and Nenon, 1990).

TABLE 5
Effect of an extremely high temperature (40°C) to which *Protopulvinaria pyriformis* was subjected for 24 h prior to parasitization by *Encyrtus infelix*, on the incidence of parasitoid egg encapsulation[1]

| Host plant | Rearing temperature °C | High temperature exposure | Number of parasitized scales dissected | Parasitoid eggs: Total number observed | Encapsulated n | Encapsulated % ± S.D. | Parasitized scales with encapsulated eggs only[2] n | % ± S.D. |
|---|---|---|---|---|---|---|---|---|
| *Hedera helix* | 24 | – | 148 | 190 | 189 | 99.8 ± 0.3a | 151 | 99.7 ± 0.5a |
| | 28 | – | 444 | 821 | 789 | 94.6 ± 3.0a | 413 | 89.9 ± 5.8a |
| | 24 | + | 304 | 780 | 523 | 64.2 ± 14.5b | 104 | 34.3 ± 8.3b |
| *Fatsia japonica* | 24 | – | 435 | 680 | 676 | 99.2 ± 0.8a | 433 | 98.9 ± 1.0a |
| | 28 | – | 399 | 519 | 519 | 100a | 399 | 100a |
| | 24 | + | 251 | 533 | 348 | 63.7 ± 16.8b | 120 | 50.0 ± 10.4b |

[1]Within columns, means followed by the same letter do not differ significantly ($P = 0.05$), Duncan's Multiple Range Test.
[2]Efficient encapsulation.

### IV. Encapsulation of *E. infelix* eggs by *P. pyriformis*

*Encyrtus infelix* readily oviposited in second and third instar nymphs as well as in young and preovipositing females of *P. pyriformis*. Usually one, but sometimes up to eight or more eggs were oviposited in a single scale. Most of these eggs, however, became encapsulated at 24 or 28°C (Table 5). Newly hatched parasitoid larvae (up to five per scale), which probably had managed to escape from egg capsules, were observed in fewer than 5% (n = 26) of the overall parasitized scales dissected 10 days after parasitism. However, only in four parasitized scales was *E. infelix* able to complete its development and four adult wasps emerged; the rest of the developing larvae died within 2–3 weeks after hatching.

Females of *P. pyriformis* which prior to their parasitism by *E. infelix* had been exposed to 40°C for 24 h ("treated" scales) lost much of their ability to encapsulate parasitoid eggs. This was manifested by a significant reduction in the percentage of both eggs encapsulated and efficient encapsulation (Table 5).

A significant reduction in the ability of *C. hesperidum* and *S. coffeae* to encapsulate eggs of *M. swirskii* was likewise demonstrated, following the use of the same procedure (Blumberg, 1976, 1982).

The ability of *E. infelix* to develop successfully in many parasitized *P. pyriformis* after intentionally reducing the incidence of parasitoid encapsulation therefore indicates that the degree of encapsulation of parasitoid eggs by a given host insect is not a reliable index for the overall suitability of the host and parasitoid. This was also demonstrated by Bartlett and Ball (1966) for several coccid hosts and their parasitoid *Metaphycus luteolus* (Timberlake).

### V. Encapsulation of *E. infelix* eggs by *C. hesperidum, P. nigra,* and *P. urbicola*

Oviposition by *E. infelix* in *C. hesperidum, P. nigra,* and *P. urbicola* resulted in a complete egg encapsulation: in *C. hesperidum,* 250 eggs in 69 scales; in *P. nigra,* 114 eggs in 67 scales; and in *P. urbicola,* 160 eggs in 118 scales. This complete encapsulation, which prevented any parasitoid development, indicates that none of the additional coccids examined can serve as an alternative host for the two *Encyrtus* species studied. In this regard, Thorpe (1936) also found that *E. infelix* can attack *C. hesperidum,* but indicated that it was an unusual host.

ACKNOWLEDGEMENTS

The authors are grateful to Mr. A. Rubin, Biological Control Laboratory, 1 Keren Hayesod, Giv'at Shmuel, Israel, for providing adults of *E. infelix* which were used to establish the insectary culture of the parasitoid. The assistance of Dr. M. Kehat, Department of Entomology, A.R.O., Bet Dagan, in the statistical analysis of the results is gratefully acknowledged. We also thank Dr. G.L. Prinsloo, Plant Protection Research Institute, Pretoria, South Africa, and Dr. Q. Argaman, Plant Protection and Inspection Department, Ministry of Agriculture, Bet Dagan, Israel, for identifying the two species of *Encyrtus.*

REFERENCES

**Annecke, D.P.** 1964. The encyrtid and aphelinid parasites (Hymenoptera: Chalcidoidea) of soft brown scale, *Coccus hesperidum* Linnaeus (Hemiptera: Coccidae) in South Africa. *Entomology Memoirs, Department of Agricultural Technical Services, Republic of South Africa* 7: 1–74.

**Avidov, Z. and Harpaz, I.** 1969. Plant Pests of Israel. Israel Universities Press, Jerusalem. 549 pp.

**Bartlett, B.R.** 1978. Homoptera: Coccidae. In: Introduced Parasites and Predators of Arthropod Pests and Weeds; A World Review. Edit. C.P. Clausen. *USDA Agriculture Handbook No. 480.* pp. 57–74.

**Bartlett, B.R. and Ball, J.C.** 1966. The evolution of host suitability in a polyphagous parasite with special reference to the role of egg encapsulation. *Annals of the Entomological Society of America* 59: 42–45.

**Bess, H.A.** 1939. Investigations on the resistance of mealybugs (Homoptera) to parasitization by internal hymenopterous parasites, with special reference to phagocytosis. *Annals of the Entomological Society of America* 32: 189–226.

**Blumberg, D.** 1976. Extreme temperatures reduce encapsulation of insect parasitoids in their insect hosts. *Experientia* 32: 1296–1397.

**Blumberg, D.** 1977. Encapsulation of parasitoid eggs in soft scales (Homoptera: Coccidae). *Ecological Entomology* 2: 185–192.

**Blumberg, D.** 1982. Further studies of the encapsulation of *Metaphycus swirskii* by soft scales. *Entomologia Experimentalis et Applicata* 31: 245–248.

**Blumberg, D.** 1988. Encapsulation of eggs of the encyrtid wasp, *Metaphycus swirskii*, by the hemispherical scale, *Saissetia coffeae*: Effect of host age and rearing temperature. *Entomologia Experimentalis et Applicata* 47: 95–99.

**Blumberg, D.** 1991. Seasonal variations in the encapsulation of eggs of the encyrtid parasitoid *Metaphycus stanleyi* by the pyriform scale, *Protopulvinaria pyriformis*. *Entomologia Experimentalis et Applicata* 58: 231–237.

**Blumberg, D. and DeBach, P.** 1981. Effects of temperature and host age upon the encapsulation of *Metaphycus stanleyi* and *Metaphycus helvolus* eggs by brown soft scale *Coccus hesperidum*. *Journal of Invertebrate Pathology* 37: 73–79.

**Blumberg, D. and Luck, R.F.** 1990. Differences in the rates of superparasitism between two strains of *Comperiella bifasciata* (Howard) (Hymenoptera: Encyrtidae) parasitizing California red scale (Homoptera: Diaspididae): an adaptation to circumvent encapsulation? *Annals of the Entomological Society of America* 83: 591–597.

**Blumberg, D. and Swirski, E.** 1977. Mass breeding of two species of *Saissetia* (Hom. Coccidae) for propagation of their parasitoids. *Entomophaga* 22: 147–150.

**Bodenheimer, F.S.** 1951. Citrus Entomology in the Middle East. W. Junk, The Hague.

**Brewer, R.H.** 1971. The influence of the parasite *Comperiella bifasciata* How. on the populations of two species of armoured scale insects, *Aonidiella aurantii* (Mask.) and *A. citrina* (Coq.) in South Australia. *Australian Journal of Zoology* 19: 53–63.

**Copland, M.J.W. and Ibrahim, A.G.** 1985. Biology of glasshouse scale insects and their parasitoids. In: Biological Control. The Glasshouse Experience. Edit. N.W. Hussey and N. Scopes. Cornell University Press, Ithaca, New York. pp. 87–90.

**Dijkerman, H.J.** 1990. Suitability of eight *Yponomeuta* species as hosts of *Diadegma armillata*. *Entomologia Experimentalis et Applicata* 54: 173–180.

**Duncan, D.B.** 1955. Multiple range and multiple F tests. *Biometrics* 11: 1–42.

**Giordanengo, P. L and Nenon, J.P.** 1990. Melanization and encapsulation of eggs and larvae of *Epidinocarsis lopezi* by its host *Phenacoccus manihoti*; effects of superparasitism and egg laying patterns. *Entomologia Experimentalis et Applicata* 56: 155–163.

**Maple, J.D.** 1947. The eggs and first instar larvae of Encyrtidae and their morphological adaptations for respiration. *University of California, Publications in Entomology* 8: 25–122.

**Messenger, P.S. and van den Bosch, R.** 1971. The adaptability of introduced biological control agents. In: Biological Control. Edit. C.B. Huffaker. Plenum Press, New York. pp. 68–92.

**Muldrew, J.A.** 1953. The natural immunity of the larch sawfly (*Pristiphora erichsonii* (Htg.)) to the introduced parasite *Mesoleius tenthredinis* Morely, in Manitoba and Saskatchewan. *Canadian Journal of Zoology* 31: 313–332.

**Nikolskaja, M.N.** 1952. The chalcid fauna of the USSR (Chalcidoidea). (Translated from Russian). Israel Program for Scientific Translations, Jerusalem. pp. 1–593.

**Peck, O.** 1963. A catalog of the nearctic Chalcidoidea (Insecta: Hymenoptera). *The Canadian Entomologist, Supplement* 30: 1–1092.

**Prinsloo, G.L.** 1984. An illustrated guide to the parasitic wasps associated with citrus pests in the Republic of South Africa. *Science Bulletin, Department of Agriculture, Republic of South Africa* No. 402: 1–119.

**Puttler, B.** 1959. Partial immunity of *Laphygma exigua* (Hubner) to the parasite *Hyposoter exiguae* (Viereck). *Journal of Economic Entomology* 52: 327–329.

**Reed, D.K., Hart, W.G. and Ingle, S.J.** 1968. Laboratory rearing of brown soft scale and its hymenopterus parasites. *Annals of the Entomological Society of America*, 61: 1443–1446.

**Rivnay, E.** 1944. The economic status of *Coccus hesperidum* L. and its parasites in Palestine. *Journal of the Entomological Society of Southern Africa* 7: 73–81.

**Rosen, D.** 1967. The hymenopterous parasites of soft scales on citrus in Israel. *Beiträge zur Entomologie* 17: 255–283.

**Rosen, D., Harpaz, I. and Samish, M.** 1971. Two species of *Saissetia* (Homoptera: Coccidae) injurious to olive in Israel and their natural enemies. *Israel Journal of Entomology* 6: 35–53.

**Salt, G.** 1963. The defence reactions of insects to metazoan parasites. *Parasitology* 53: 527–642.

**Streams, F.A.** 1971. Encapsulation of insect parasites in superparasitized hosts. *Entomologia Experimentalis et Applicata* 14: 484–490.

**Thorpe, W.H.** 1936. On a new type of respiratory interrelation between an insect (chalcid) parasite and its host (Coccidae). *Parasitology* 28: 517–540.

**van Alphen, J.J.M. and Visser, M.E.** 1990. Superparasitism as an adaptive strategy for insect parasitoids. *Annual Review of Entomology* 35: 59–79.

**Vinson, S.B. and Iwantsch, G.F.** 1980. Host suitability for insect parasitoids. *Annual Review of Entomology* 25: 397–419.