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Biology of *Prochiloneurus insolitus* (ALAM) (Hymenoptera, Encyrtidae), a hyperparasitoid on mealybugs (Homoptera, Pseudococcidae): immature morphology, host acceptance and host range in West Africa

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The endophagous hyperparasitoid *Prochiloneurus insolitus* (ALAM) was offered various stages of *Epidinocarsis lopezi* (DE SANTIS), a primary parasitoid of the cassava mealybug (CM) *Phenacoccus manihoti* (MATILE-FERRERO). Embryos were surrounded by a trophamnion. Larval development involved four instars, and adult females emerged after 11.2 days at 27 °C. In a choice experiment parasitized and unparasitized CM of different instars were attacked with equal frequency, though no egg was ever laid into unparasitized CM. Stung CM without an immature wasp suffered from increased mortality and had a reduced oviposition capacity compared to those not attacked by the hyperparasitoid. CM wax and ovisacs were the main attractant in locating the secondary host, and older CM instars were preferred over younger ones. The attack of *P. insolitus* is stimulated by physical cues from unrelated secondary hosts. Oviposition is induced by chemical stimuli of primary encyrtid hosts.

INTRODUCTION

The encyrtid genus *Prochiloneurus* SILVESTRI is cosmopolitan. All 32 described species are hyperparasitoids (NOYES & HAYAT, 1984). *P. insolitus* described from India (ALAM, 1961), has been found throughout tropical Africa to attack parasitoids (mainly *Anagyrus* spp.) of the cassava mealybug (CM) *Phenacoccus manihoti* MATILE-FERRERO (Hom.: Pseudococcidae) (MATILE-FERRERO, 1977; FABRES & MATILE-FERRERO, 1980; BOUSSIENGUET, 1986). The South American parasitoid *Epidinocarsis lopezi* (DE SANTIS) (Hym.: Encyrtidae) was introduced into Africa for the biological control of CM, a major pest on cassava *(Manihot esculenta* CRANTZ) (HERREN & NEUENSCHWANDER, 1991). In West Africa, *P. insolitus* immediately became one of its most abundant indigenous hyperparasitoids (NEUENSCHWANDER *et al.*, 1987). Survey data suggested that the entire guild of hyperparasitoids acted in a density-dependent way in relation to their host population, leading to relatively low hyperparasitism rates wherever *E. lopezi* had brought the CM under control (NEUENSCHWANDER & HAMMOND, 1988; NEUENSCHWANDER *et al.*, 1989a; 1990).

Little is known about the biology, behaviour and the exact ecological role of these hyperparasitoids. As a first step in their study, the morphology and biology of *P. insolitus,* with particular reference to host finding and acceptance behaviours on *E. lopezi,* are presented and related to field records on indigenous hosts.

MATERIAL AND METHODS

Laboratory observations

The *P. insolitus* culture was started with adult wasps captured on cassava in the field. The hyperparasitoids were reared on CM mummies containing *E. lopezi,* obtained from an insectary culture (NEUENSCHWANDER *et al.*, 1989b). The wasps used in the experiment were randomly collected from the rearing containers on the first day after emergence and fed on diluted honey. To enhance host searching, they were isolated from all hosts for 24 hours.

Each wasp was offered 15 potential hosts in a Petri dish of 9 cm diameter and 1.5 cm height. They represent the following combinations of immature *E. lopezi* and CM instars (L_1-L_4), as defined by KRAAIJEVELD & VAN ALPHEN (1986) and LÖHR *et al.* (1989), together with the relevant unparasitized CM serving as a control (see abscissa in Fig. 2): (1) L_1 unparasitized; (2) L_2 unparasitized or (3) containing an *E. lopezi* egg, or (4) larva; (5) L_3 unparasitized, (6) with egg, or (7) larva, or (8) mummy, i.e. the hardened skin of the CM containing an old larva or pupa of *E. lopezi;* (9) L_4 without ovisac, with the same (10, 11, 12) categories as for the L_3; (13) L_4 with ovisac either unparasitized or (14) mummified. Each time the ovisac of these L_4 was attacked by the hyperparasitoid the choice was attributed to (unparasitized) CM eggs (15). This could be followed by a sting on the L_4 with (13) or without parasitoid (14).

The CM containing a parasitoid egg were obtained on the same day an *E. lopezi* female was observed under a binocular microscope stinging a host. To provide CM containing parasitoid larval instars, CM were kept 2–4 days after the observed oviposition by *E. lopezi* before being used in the choice experiment. For safe recognition, the CM were marked by mutilating either one antenna or one leg, a procedure which was varied randomly among set-ups. In order to secure the mummies they were glued to the bottom of the Petri dish with diluted, water-soluble glue that had no noticeable deleterious effect on the wasps.

For each experiment, a single female *P. insolitus* was introduced into the Petri dish containing the 15 prepared hosts and its foraging behaviour observed. After one hour, the wasp was replaced for each of the 150 replicates. Record was made of the number of stung CM including stinging time. Stung CM were replaced by others of the same instar and treatment. A stinging action sometimes included several ovipositor insertions and was considered terminated only when the hyperparasitoid left the host. Behaviour such as palpation, tapping and drumming with the antennae was recorded but not timed. For eventual insect emergence, all stung insects from 75 randomly chosen replicates were reared in sleeve cages on potted cassava plants in a temperature chamber at 27 ± 0.5 °C (12L/12 D photoperiod). Oviposition capacity and life span of stung unparasitized CM were compared to those of control CM.

Life cycle and immature morphology of *P. insolitus* were followed by dissecting stung CM from the remaining 75 repetitions in a saline solution under a binocular microscope 0 to 8 days after attack. Eventual melanization of host tissues due to encapsulation (SALT, 1956; SULLIVAN & NEUENSCHWANDER, 1988) was also recorded.

The number of stings on parasitized and unparasitized CM of the same age observed during one hour of exposure were compared by means of a chi-square test with one degree of freedom, at $P < 0.05$, based on the pooled data of all replicates. Probing time is given as mean ± standard error; no analysis of variance was

done because of the highly different number of stings observed on the different hosts.

Field observations

From 1988 to 1990 pseudococcids were collected in south-western Nigeria and the south of the Republic of Benin from various host plants. This search was intensified at the end of each dry season (February-March), when mealybug populations are abundant. Plant material infested with Coccoidea and other potential hosts was held in aerated plastic boxes for subsequent emergence of Hymenoptera. Individual mummies were kept separately in gelatine capsules.

RESULTS

Morphology and life-cycle

The egg of *P. insolitus* is found floating free in the haemolymph of *E. lopezi,* its primary host. The freshly deposited egg is elongated and stalked, with an average size of 0.11 by 0.04 mm (Fig. 1). The yellow, translucent chorion can easily be distinguished from the opaque fluid of the host. Up to eclosion, the egg increases its size ca. 3-fold by absorbing host haemolymph through the chorion's trophic membrane, the trophamnion, while the stalk remains unchanged.

Four larval instars were observed. The first instar larva is still surrounded by the trophamnion composed of few but relatively large cells arranged in a regular geometric pattern. No respiratory features of the larva could be observed at 40 times magnification.

Two to three days after oviposition, the second instar larva appeared. It disrupts the trophamnion so that its head and tail protrude from the surrounding membrane. The larva has a bent tail allowing a slight motion. The last abdominal segment bears the shed exuvia of the first instar. The head is well differentiated and prominent. With continuous nutrient uptake from the host, the middle-gut becomes visible. Tracheae are noticeable as a pair of lateral trunks.

In the third instar larva, the steady growth causes a fragmentation of the trophamnion, which becomes a mass of amorphous particles floating in the haemolymph of the primary host. Respiratory structures are now well developed, represented by nine pairs of spiracles joined to a longitudinal trunk system. The tail is less obvious than in the second instar; it now carries an additional exuvia.

The fourth instar larva grows fast from 0.55×0.15 mm to 0.96×0.36 mm, and the caudal appendage is absent. The previously endophagous larva now feeds with the body partly exposed externally. After the primary host has been consumed and reduced to a shrunken skin, the larva becomes still, releasing its meconium before pupation. At this stage, even those CM hosts that were still mobile, had hardened to mummies, in which pupation of *P. insolitus* took place.

The adult hyperparasitoid emerged by slicing (with its mandibles) an irregular hole, with ragged edges, anywhere in the mummy. Emergence of *E. lopezi,* by comparison, is done by pushing open an exit cap, leading to a clean circular hole at the posterior end of the mummy.

At 27 °C the developmental time from egg to imago was 11.2 ± 0.12 S. E. ($n = 99$) days for females, compared to only 10.4 ± 0.13 S. E. ($n = 65$) days for the smaller-sized males. The sex ratio was 1.7 females to 1.0 males ($n = 164$) and mating occurred soon after emergence.

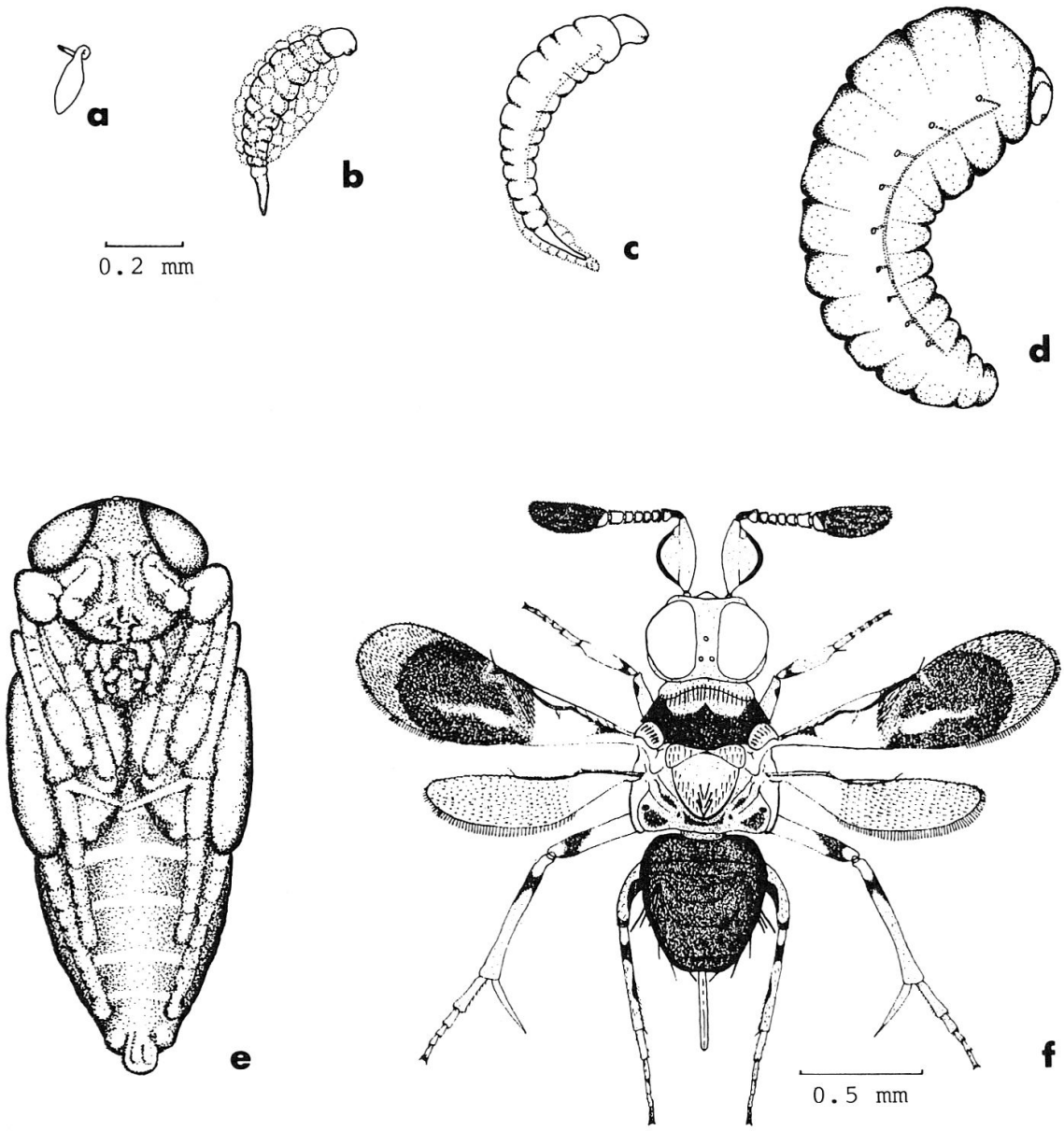

Fig. 1. Morphology of *Prochiloneurus insolitus:* a) egg, b) second-instar larva surrounded by trophamnion, c) third-instar larva, d) fourth-instar larva, e) pupa, f) adult female.

A single egg is laid per ovipositor insertion into the body of the primary host, in this case *E. lopezi.* The egg is either deposited while the CM is still alive, to develop at a later stage or into the already mummified CM. Mummies with an older conspecific larva are rejected following probing with the ovipositor. However, superparasitism has been observed when the first hyperparasitoid immature was so small that the female investigating the host with her ovipositor probably missed it. Since *P. insolitus* is strictly solitary all supernumerary eggs and larvae die. Stinging into unparasitized CM is frequent; but oviposition has never been observed under these circumstances. The females do not host-feed; but they readily accept honeydew ejected for defense by an attacked mealybug.

Host selection

After encountering either mealybug wax, an ovisac, or a mummified CM in the Petri dish, the *P. insolitus* female stopped and rapidly tapped the integument of the host with the antennae. This was interpreted as a registration of chemotactile stimuli. It then turned around and stung when resistance was encountered, whether it was the Petri-dish bottom or the front of the secondary host.

While stinging, the ovipositor displayed alternate rotations of ca. 270 degrees. The ovipositor was thrust in all directions, probably to locate the host in the body of the mealybug. Egg deposition took only a few seconds. After oviposition, the female invariably wiped off the ovipositor on the dorsum of the CM, a behaviour not observed when no egg was deposited.

Considerably more time was spent by the *P. insolitus* female on mummified CM than on living ones (Table 1). From the total recorded time, 68% was devoted to hyperparasitize mummies, which accounted for only 20% of all host combinations. The drilling action on mummies represented the major time investment, the actual oviposition taking less than 60 seconds. By contrast, host location and oviposition in a mobile mealybug required less energy and time than on mummies, thus making the search in CM attractive despite a lower likelihood of finding a host. The amount of time spent probing unparasitized CM, which move around and are therefore encountered more frequently, was substantial.

Tab. 1. Mean probing times, in seconds, of female *Prochiloneurus insolitus* on cassava mealybugs (CM) of different instars (L_1-L_4) containing different stages of the primary parasitoid *Epidinocarsis lopezi*.

CM	*E. lopezi*	n	mean	± S.E.
L1	none	1	15	- -
L2	none	5	144	59.4
	egg	8	43	7.4
	larva	9	46	7.4
L3	none	8	93	16.3
	egg	13	132	46.9
	larva	23	68	33.1
	mummy	11	206	18.2
L4	none	46	93	15.2
	none + ovisac	220	88	5.4
	egg	53	69	11.0
	larva	72	84	11.5
	mummy	54	229	14.8
	mummy + ovisac	227	281	11.6

During 150 observation hours, a total of 1490 stings were registered (Fig. 2). Evidently, the different CM instars were attacked at highly different rates. Ovisacs received 49% of all attacks. While all other hosts including control insects were offered only once, CM ovisacs were represented twice, namely with parasitized and with unparasitized L_4. These stings on CM that harboured no suitable host were only of prospective nature and occurred without deep insertion of the ovipositor.

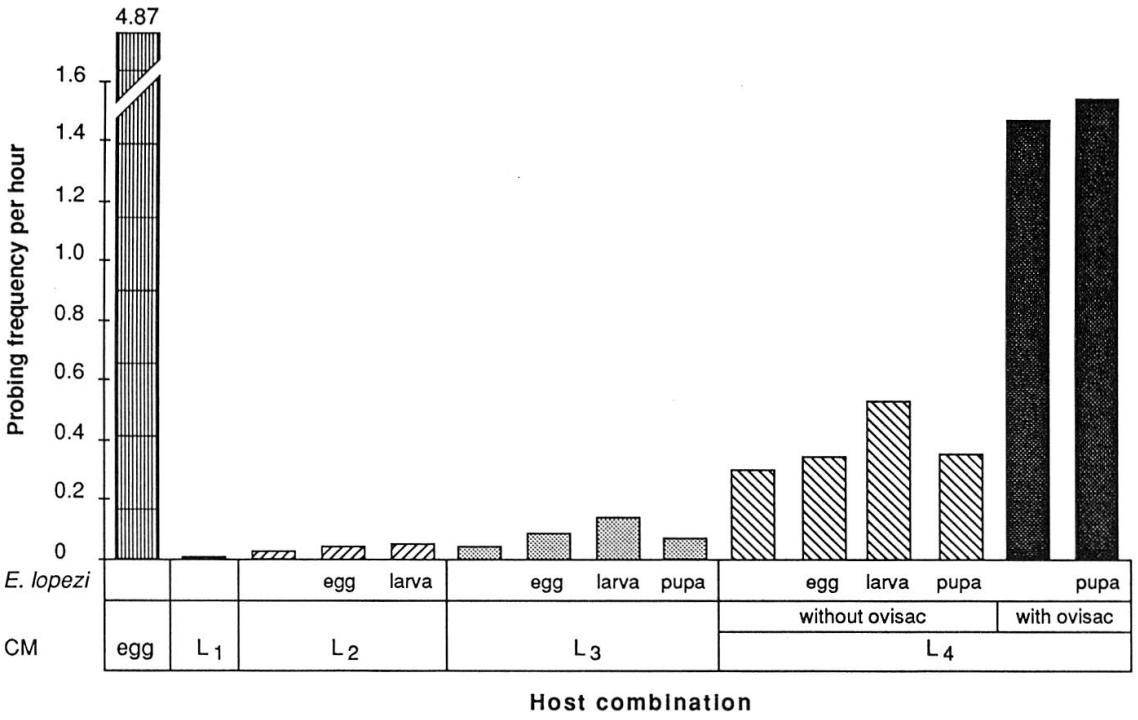

Fig. 2. Host selection by *Prochiloneurus insolitus:* Probing frequency in a choice test with different stages of primary *(Epidinocarsis lopezi)* and secondary *(Phenacoccus manihoti)* hosts.

The 759 remaining stings were on CM. Only 8% were made with the wasp on the host, while in most cases the female hyperparasitoid was positioned in front of the CM. The most attractive hosts were CM with ovisacs, i. e., mummified L_4 (30.3% out of 759) and unparasitized L_4 (29.4%) (Fig. 2). By contrast, an L_1 was chosen only once. Probing frequency increased with the instar of the CM (computed as 1, 2, 3, 4) (explained variance of the correlation $r^2 = 0.79$; $P < 0.05$; $n = 303$, L_4 with ovisacs excluded), regardless of whether the CM was parasitized or not. Thus, after the attraction exerted by egg masses, host size was the second most important factor affecting host selection.

Between parasitized and unparasitized CM of the same instar, no significant differences ($P = 0.05$) in the attack frequencies were detected (L_2 : $n = 22$, chi-square = 0.91; L_3: $n = 55$, chi-square = 2.48; L_4 without ovisac: $n = 225$, chi-square = 1.77; L_4 with ovisac: $n = 447$, chi-square = 0.11). According to rearing and dissections only 53% of all hosts examined by the hyperparasitoid were suitable for development. It is concluded that *P. insolitus* cannot determine the presence of the primary host when it attacks a CM; a preliminary examination with the ovipositor is required to detect *E. lopezi.*

Among the L_4 which were predominantly probed ($n = 103$), 33% displayed melanization though they contained no *E. lopezi.* Attacked CM of all instars ($n = 25$) had a significantly shorter life span than the unattacked control ($n = 25$), namely 9.2 days ± 0.94 S. E. compared to 20.0 days ± 0.68 S. E. ($t = 9.31$, $P < 0.05$). They also had a reduced oviposition capacity (66.8 eggs ± 11.39 S. E. as compared to 401.5 eggs ± 18.24 S. E. ($t = 15.56$, $P < 0.05$). Thus, *P. insolitus* has a direct influence on the CM, i. e. across two trophic levels.

Host range

The wide range of secondary hosts of *P. insolitus* in West Africa is shown in Table 2. Specificity at the level of the primary host is clearly expressed in that all are encyrtids parasitizing pseudococcids on various host plants. In addition, *P. insolitus* reproduced on the encyrtid *Homalotylus africanus* TIMBERLAKE in mummified coccinellid larvae attributed to *Nephus pseudococcophagus* FÜRSCH, on *Phenacoccus madeirensis* GREEN in the laboratory.

Tab. 2. Host range of *Prochiloneurus insolitus* from material sampled in SW Nigeria and in the south of the Republic of Benin.

Plant	Secondary host	Primary host
Manihot esculenta	*Phenacoccus manihoti* MAT.-FERR.	*Epidinocarsis lopezi* (DE SANTIS)
M. dichotoma		*Anagyrus* sp. 1
M. dichotoma	*Ferrisia virgata* COCKERELL	*Blepyrus insularis* CAMERON
Hibiscus sp. *Acalypha* sp.	*P. madeirensis* GREEN	*Anagyrus* sp. 2
Mangifera indica	*Rastrococcus invadens* WILLIAMS	*Gyranusoidea tebygi* NOYES
Annona muricata	*Maconellicoccus hirsutus* GREEN	*Gyranusoidea indica* SHAFEE *Anagyrus* sp. 2
Ipomea asariflora	undet. Pseudococcidae	*Anagyrus* sp. 3
Thunbergia erecta	*Nephus pseudococcophagus* FÜRSCH	*Homalotylus africanus* TIMBERLAKE

DISCUSSION

Correct attribution of published material to *P. insolitus* is difficult for taxonomic reasons. By original designation, *P. insolitus* was referred to the genus *Achrysopophagus* GIRAULT, which has become a junior genus synonym (ALAM, 1961). Further systematic revisions (HAYAT, 1981) revealed a specific synonymy with *P. metallicus* (AGARWAL), and the taxon has also been identified as *P. taurus* (GIRAULT) and *P. pulchellus* SILVESTRI. Frequent colour variations of the head, thorax, and the funicle segments further complicate identification of *P. insolitus* (J. S. NOYES, pers. comm.).

The genus *Prochiloneurus* is hyperparasitic, via other encyrtids, on various families of Coccoidea, mainly Pseudococcidae and Coccidae, but also on Coccinellidae (NOYES & HAYAT, 1984). For *P. insolitus,* the only available host record, apart from those on CM parasitoids (MATILE-FERRERO, 1977; FABRES & MATILE-FERRERO, 1980; BOUSSIENGUET, 1986; NEUENSCHWANDER *et al.,* 1987; BIASSANGAMA *et al.,* 1989) comes from India (HAYAT, 1981). Only the secondary hosts are listed, namely *Centrococcus insolitus, Centrococcus* spp. *Nipaecoccus virdis* (NEWSTEAD), *Nipaecoccus* spp., the margarodid *Icerya aegyptica* (DGL.), and several undetermined coccids. The present study complements the previous records from Africa, but it must be assumed that the host range is still larger.

Detailed information on the biology of encyrtid hyperparasitoids is scarce. In accordance with the present observation a trophamnion was found in all solitary hyperparasitic encyrtids (CLANCY, 1946; WESELOH; 1969). Further studies are needed to determine specificity and importance.

Host acceptance is the result of a chain of decisions guiding the wasp from host selection to oviposition. In the present choice experiment, arrestment was facilitated by CM wax, and it was observed that wax from other pseudococcids had the same effect (G. GOERGEN, unpubl. results). By contrast the behaviour of *E. lopezi* in searching for hosts in the olfactometer proved to be influenced only by CM wax, while synomones from related species were ineffective (LANGENBACH & VAN ALPHEN, 1986). The results of the choice experiment suggest an unspecific attraction of *P. insolitus* to mealybugs leading to a probing sting. Parasitized mealybugs are thereby not distinguished from unparasitized ones.

Probing behaviour is prolonged when the ovipositor encounters a hard surface, as is the case with a mummy. This physical stimulus is so strong that even empty mummies are attacked. The final decision to oviposit is probably induced by detecting a soft-bodied primary host inside the hardened mummy. When *P. insolitus* stings an unparasitized CM, its ovipositor also penetrates soft-bodied tissues, as witnessed by subsequent melanization of gut and ovaries. Wounding of such tissues without oviposition by the wasp is known to lead to melanization also in primary parasitoids (SULLIVAN & NEUENSCHWANDER, 1988). This physical setup, however, is not sufficient to induce oviposition. Thus, it is concluded that the stimulus for oviposition is of a chemical nature specific to encyrtids and is perceived by chemoreceptors on the tip of the ovipositor.

Such receptors were found to function in host discrimination of *Alloxysta (Charips) victrix* WESTWOOD (Hym.; Cynipidae), an internal aphid hyperparasitoid (GUTIERREZ, 1970). WESELOH (1969) arrived at the same conclusion for *Cheiloneurus noxius* COMPERE (Hym.; Encyrtidae), a closely related hyperparasitoid of *P. insolitus* attacking coccid scales. Similarly, sensory receptors on the ovipositor, used to avoid superparasitism in solitary primary parasitoids, were described (LE RALEC & WAJNBERG, 1990).

The chemical stimulus coming from an internal encyrtid host seems to have priority over the physical stimulus of the secondary host. Thus, *P. insolitus* also reproduces on an encyrtid parasitoid of coccinellid larvae, with mummies that resemble those of the CM. Similarly, *P. aegyptiacus* (MERCET) is a common hyperparasitoid on both coccinellid larvae and mealybugs (NEUENSCHWANDER *et al.*, 1987). The positive response to a physical stimulus common to unrelated species explains the recorded broad spectrum of secondary hosts of *P. insolitus* (Table 2).

Because of its versatility, the ecological role of *P. insolitus* is difficult to assess. In the CM system, its impact must be evaluated considering the effect upon both the primary and the secondary hosts. For the CM population, the attack of *P. insolitus* caused injuries, subsequently expressed as a shorter life-span and reduced oviposition capacity similarly to those measured for *E. lopezi* when it stings a CM not used as a host (LÖHR *et al.*, 1988). The overall importance of this phenomenon remains to be measured.

The behavioural sequence leading to oviposition indicates that finding hidden encyrtid hosts requires a great investment of time and energy. This is compensated for by the observed production of tiny alecithal eggs, which are characterized by trophamnionic growth (GAULD & BOLTON, 1988). This economic egg production suggests that the reproductive potential of *P. insolitus* is not egg-limited, but time-limited. Thus, the searching capacity of various hyperparasitoids has been compared to appraise their role in an ecosystem (KFIR *et al.*, 1976).

Attempts to directly evaluate the effect of hyperparasitoids on *E. lopezi* in the field did not lead to a conclusive answer (IZIQUEL & LE RÜ, 1989). Long-term field studies show, however, that hyperparasitism did not prevent effective biological control by *E. lopezi* (NEUENSCHWANDER *et al.*, 1989a; HAMMOND & NEUENSCHWANDER, 1990) with a hyperparasitoid fauna, in which *P. insolitus* averaged 60.6% (NEUENSCHWANDER & HAMMOND, 1988). How far *E. lopezi*'s efficiency is hampered by hyperparasitoids will be determined by manipulating insect populations of all trophic levels and by adding the present data, together with those from life-table studies, to an existing multitrophic simulation model (GUTIERREZ *et al.*, 1988a, b).

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