Influence of egg load and oviposition time interval on the host discrimination and offspring survival of *Anagyrus pseudococci* (Hymenoptera: Encyrtidae), a solitary endoparasitoid of citrus mealybug, *Planococcus citri* (Hemiptera: Pseudococcidae)

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Abstract

Oviposition and host discrimination behaviour of unmated *Anagyrus pseudococci* (Girault), an endoparasitoid of the citrus mealybug *Planococcus citri* (Risso), were investigated in the laboratory. Female parasitoids were able to discriminate between parasitized hosts and healthy ones. The mean number of ovipositions was significantly higher in unparasitized than in parasitized hosts. Conspecific-superparasitism occurred more often than self-superparasitism. Changes in consecutive ovipositions over three hours by *A. pseudococci* suggested that egg load influenced the discrimination behaviour of the parasitoids, with females which had low egg loads mostly avoiding oviposition in already parasitized hosts at time intervals ranging from 0 h to 96 h, and distributing their eggs in the high quality (unparasitized) hosts. The parasitized hosts were rejected more commonly through antennal perception of external markers than during ovipositor probing which could have encountered internal markers but this relationship changed with increasing time after oviposition. The parasitoid's oviposition rate in unparasitized and conspecific-parasitized hosts varied at the different oviposition time intervals when the females had fewer eggs in the ovaries. Percentage emergence of parasitized offspring was not significantly influenced by whether they developed in single or superparasitized mealybugs. The significance of host discrimination by *A. pseudococci* is discussed.

Introduction

The parasitoid *Anagyrus pseudococci* (Girault) (Hymenoptera: Encyrtidae) is a dominant primary parasitoid of the citrus mealybug, *Planococcus citri* (Risso) (Hemiptera: Pseudococcidae) (Summy *et al.*, 1986; Moore, 1988; Tingle & Copland, 1988, 1989). The parasitoid is Mediterranean in origin and is now used widely as a biocontrol agent of mealybugs.

Parasitoid females might be expected to exhibit oviposition preference for hosts that provide higher reproductive success (Charnov & Skinner, 1985; Waage,

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1986). Superparasitism in solitary parasitoids must lead to the elimination of supernumeraries either by some form of physiological suppression or by physical combat between the larvae (Fisher, 1971; Vinson & Iwantsch, 1980; Mackauer, 1990). Thus, parasitoid females that do not gain any reproductive success by superparasitism should avoid such behaviour (Bakker *et al*., 1985; Mackauer, 1990). The ability of a parasitoid to distinguish between unparasitized and parasitized hosts is termed 'host discrimination' and is common in insect parasitoids (van Lenteren, 1981; van Alphen & Visser, 1990). Host discrimination plays an important role in the population dynamics of both host and parasitoid. Because superparasitism is associated with both costs and benefits, both of which are condition-dependent, the benefits exceed the costs when hosts are scarce and parasitoids may oviposit in already parasitized hosts. However, when high quality hosts are abundant, the costs exceed the benefits and the parasitoids are then predicted to avoid ovipositing in already parasitized hosts which might cause possible loss of offspring and wasted search time (van Lenteren, 1981). The behaviour is termed self-discrimination when a female recognizes hosts previously parasitized by herself, and conspecific-discrimination when it concerns hosts parasitized by another female of the same species (Mackauer, 1990).

The decision of a parasitoid to oviposit in parasitized hosts may be influenced by both host availability and quality (van Lenteren, 1981; van Dijken & Waage, 1987), external and internal markers (Chow & Mackauer, 1986; Hofsvang, 1988), the physiological condition of the parasitoids (including the supply of mature eggs) (Volkl & Mackauer, 1990; Rosenheim & Rosen, 1991; Minkenberg *et al*., 1992) and the probability of offspring survival (Chow & Mackauer, 1986; Waage, 1986). The time interval since the previous oviposition may also influence the parasitoid's decision to oviposit in parasitized hosts (Chow & Mackauer, 1986), because any external marking of hosts during oviposition may not remain effective for more than a few days, and the females may then detect whether a host is parasitized by internal markers due to the quality of host changing during the growth of the parasitoid larva within the host. These external and internal markers may be detectable by both the same individual and by conspecific parasitoids (Volkl & Mackauer, 1990).

Little is known about host discrimination by *A. pseudococci* and this study examines: (i) whether *A. pseudococci* can recognize parasitized hosts and avoid superparasitism; (ii) whether the parasitoid can discriminate between self- and conspecific-parasitized hosts; (iii) the oviposition pattern in parasitized and unparasitized mealybugs at consecutive ovipositions; (iv) the possible effect of egg load on the frequency of oviposition in previous parasitized hosts; (v) the influence of the time interval that has elapsed since the first oviposition on host discrimination; (vi) the role of internal and external markers on this discrimination; and (vii) the percentage emergence of the parasitoid from single and superparasitized *P. citri.*

Materials and methods

Insect cultures

Anagyrus pseudococci was obtained originally from Israel and has been maintained in culture at Wye College for many years and is reared in the laboratory in small ventilated plastic cages (173 × 115 × 65 mm). *Planococcus citri* was collected from the Wye College Conservatory and kept in culture on sprouting potatoes. The mealybug and parasitoid cultures were maintained at 26 ± 1°C, 45–60% r.h. and 12L:12D photoperiod of 12.7 watt/m^2 light intensity. Pre-ovipositing adults of *P. citri* were used in this study. The newly moulted individuals were recognized by their size and the presence of exuviae.

Parasitoid and host quality

Newly emerged, female parasitoids were placed with an excess of mealybug hosts for two days for oviposition experience and also provided with 50% honey solution as food. Females begin ovipositing from the first day of eclosion (unpublished observation). Experienced, unmated female parasitoids were used throughout this study to avoid any possible bias that may have resulted from differences in the reproductive values of unfertilized (= male) and fertilized (= female) eggs (Waage, 1986) or from the sex related differential mortality of the parasitoids in different qualities of hosts. Different qualities (condition of hosts with regards to parasitism) of *P. citri*, such as unparasitized (i.e. had no previous exposure to any parasitoids), self-parasitized and conspecific-parasitized, were used. Experiments were carried out in the laboratory at 23°C with 12 watt/m^2 light. A Petri-dish of 5.5 cm diameter with a lid was used as the oviposition arena. The parasitized hosts were obtained by exposing an individual mealybug to a parasitoid female for the deposition of a single egg. Successful ovipositions were recognized by the pumping movement of the abdomen after the insertion of the ovipositor and by the egg stalk protruding externally from each host which was visible using a microscope and fibre optic cool light.

Oviposition observations

In all experiments, the parasitoid was introduced into the oviposition arena at a location equidistant from the unparasitized and parasitized mealybugs. Once an egg was laid in a mealybug host, the parasitoid was carefully removed and placed in another Petri-dish containing two similarly treated host individuals.

Host discrimination (choice test) and consecutive oviposition pattern

In each two-choice test experiment, the ability of *A. pseudococci* to discriminate between: (i) unparasitized and conspecific-parasitized mealybugs; and (ii) self- and conspecific-parasitized mealybugs were examined. A female parasitoid was introduced into the oviposition arena containing two mealybugs (one from each host category). Parasitized hosts were used fresh <3 h after oviposition. Oviposition activity of three-day-old parasitoids deprived of hosts for 24 h was observed individually between 12.00 and 15.00 h, during which females could lay a maximum of ten eggs (unpublished observation). The consecutive oviposition pattern of *A. pseudococci* in unparasitized and conspecific-parasitized hosts was determined using up to nine consecutive ovipositions.

Effect of egg load on host discrimination

In the first set of experiments, the successive oviposition pattern of *A. pseudococci* occurred with equal frequency in parasitized and unparasitized hosts particularly in their early oviposition bouts. A second experiment was conducted to examine whether the superparasitism behaviour of parasitoids differed depending on the number of mature eggs in their ovaries. Following two days of host experience, four-day-old females were divided into two groups to obtain parasitoids of variable egg loads, one group being deprived of hosts for 36 h while the other group was deprived for only 12 h. Following oviposition, the parasitoids were dissected and those which had egg-loads from five to nine were considered as 'low' and those with 10+ eggs as 'high' egg-load groups, respectively. The effect of the time between ovipositions on the discrimination between unparasitized and conspecific-parasitized mealybugs was studied using these variable egg-load parasitoids. The conspecific-parasitized individuals were used 0–2, 24–26, 48–50, 72–74 and 96–98 h after the first parasitization. A female was introduced into the oviposition arena containing one unparasitized and one conspecific-parasitized mealybug from one of the above time intervals and then observed for the first four ovipositions. The following types of parasitoid behaviour were recorded: (i) antennal contacts; (ii) short probes with the ovipositor; and (iii) oviposition. The parasitoids were then frozen and dissected later that day to quantify egg-load. The ovaries were placed in a drop of insect saline solution on a microscope slide and the number of mature oocytes counted (i.e. only those positioned at the base of the ovarioles and of full size were considered mature, not those associated with nurse cells) and added to the number of eggs laid to determine the egg-load of the parasitoids.

Statistical analysis

Twenty replications were made of each experiment. Discrimination by the parasitoids between two host types was compared with the Mann-Whitney test. The relationship between percentage oviposition in unparasitized hosts and consecutive oviposition bouts was determined by a regression analysis. The influence of egg-load and the time between ovipositions on discrimination were analysed using analysis of variance (PROC GLM). Means were separated using Fisher's Pairwise comparison at the $P = 0.05$ level. Discrimination through antennation and probing at the different time intervals and the percentage emergence from hosts of different qualities were compared using Chi-square analysis.

Results

Oviposition and host discrimination

The initial response of *A. pseudococci* on encountering an individual host of *P. citri* was to examine it by drumming with the antennae. After antennation, the females either moved away (antennal rejection) or stayed near the host (antennal acceptance). Antennal acceptance was followed by probing the host. When probing lasted for a very short time (<5 s) with no pumping movement and no trace of parasitoid eggs when the host was dissected then the encounter was classified as a 'probing rejection'. When probing was followed by a pumping movement of the abdomen the encounter was classified as 'probing acceptance'. The mean number of successful ovipositions by three-day-old females in different types of mealybug host is presented in table 1. There were significant differences between the treatments. Oviposition was highest (U = 605.0; $P < 0.01$) in unparasitized hosts. In a choice between self-parasitized and conspecific-parasitized hosts, the females showed a significant preference for conspecific-parasitized hosts (U = 602.5; $P < 0.01$).

Consecutive oviposition pattern

The consecutive oviposition pattern of *A. pseudococci* in unparasitized and in 0–2-h-old parasitized hosts showed that acceptance of unparasitized hosts was greatest in the latter part of the oviposition bout (fig. 1). The regression between percentage oviposition in unparasitized hosts and consecutive oviposition bouts showed a significant linear relationship ($y = 53.1 + 5.00x$, $r^2 = 0.79$; F = 26.39; df = 8, $P < 0.01$).

Effects of egg-load and time intervals

The rejection or acceptance of parasitized hosts differed significantly with the ovarian egg-load (F = 163.75; df = 1, $P < 0.001$) (fig. 2). The parasitoids, which had a high egg-load, accepted parasitized hosts as frequently as unparasitized hosts at all intervals between oviposition but parasitoids with a low egg-load oviposited in parasitized hosts much less frequently. Figure 2 also shows greater discrimination by *A. pseudococci* at all intervals between oviposition when the females had few eggs in the ovaries (F = 4.52; df = 4, $P < 0.05$), while the parasitoids with a high egg-load did not differ significantly in the number of ovipositions in different host qualities at any time intervals (F = 0.96; df = 4, $P > 0.05$). The identification by the parasitoid of the parasitized hosts was evident either during antennation or probing. The rejection of parasitized mealybugs during antennation was more frequent than during probing in both high and low egg-load conditions (fig. 3). The decrease of antennal rejection and increase in probing rejection from 0 to 72 h time intervals was more prominent in parasitoids with low egg-loads ($\chi^2 = 21.3$, df = 4, $P < 0.01$). However, the difference was not significant in parasitoids with high egg-loads probably due to a lower number of total rejection encounters.

Table 1. Oviposition by *Anagyrus pseudococci* in pairs of *Planococcus citri*, one unparasitized and one either self- or conspecific-parasitized.

Host type	Mean number of ovipositions/ female in 3 h ± SE	Host type	Mean number of ovipositions/ female in 3 h ± SE
Unparasitized	5.4 ± 0.24	Self-parasitized	2.3 ± 0.16
Conspecific-parasitized	2.1 ± 0.19	Conspecific-parasitized	4.8 ± 0.21
Statistics	U = 605.0; ($P < 0.01$)		U = 602.5; ($P < 0.01$)

20 replicates.

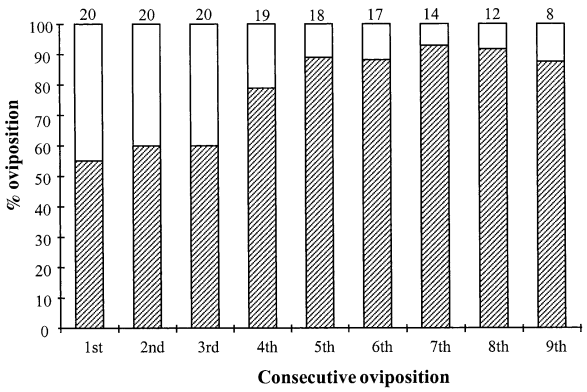

Fig. 1. The consecutive oviposition pattern of *Anagyrus pseudococci* in unparasitized (■) and conspecific-parasitized (□) *Planococcus citri* in a 3-h period of successive ovipositions. Figures above columns are number of ovipositions from 20 parasitoid individuals.

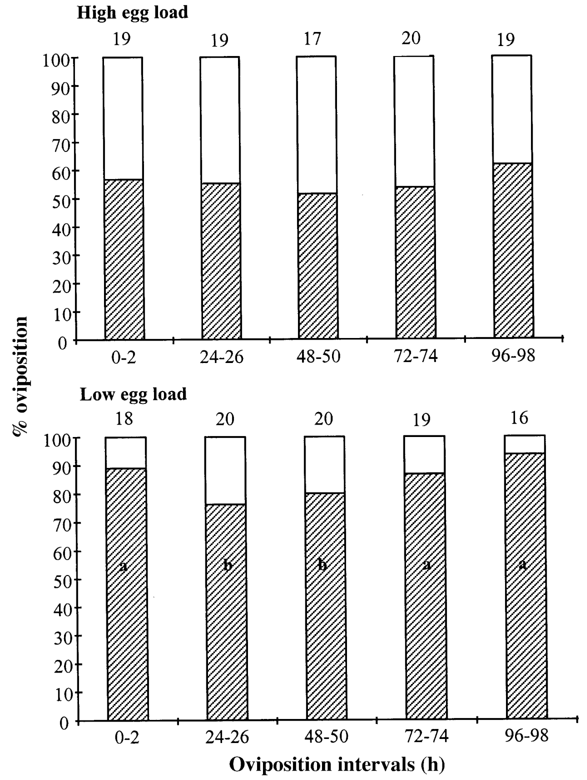

Fig. 2. Percentage of frequency of oviposition in *Planococcus citri* at different oviposition intervals by *Anagyrus pseudococci* with high (10 and above eggs) and low (5–9 eggs) egg-load. Different letters in the columns represent significant differences in between columns (Fisher's Pairwise Comparisons, at $P = 0.05$). Figures above columns are number of females observed. Each female was observed for four ovipositions in a choice test between unparasitized (■) and parasitized (□) mealybugs.

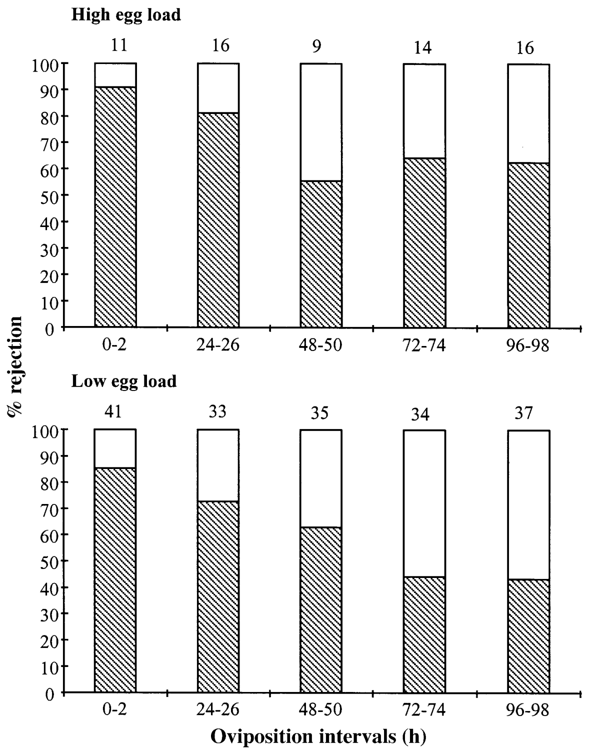

Fig. 3. Percentage of host rejected after antennation and ovipositor probing in conspecific-parasitized *Planococcus citri* by *Anagyrus pseudococci* at different oviposition intervals. ■, Rejection after antennation: percent of encounters resulting in drumming but no ovipositor insertion; □, rejection after probing: percent of encounters resulting in a short probing with the ovipositor that lasted < 5 s. Figures above columns are number of encounters resulting in rejection of the hosts.

Host suitability

There was no significant difference in the percentage emergence from parasitized hosts (i.e. with a single egg) and superparasitized hosts with two eggs (table 2).

Discussion

These laboratory studies suggest that, at the time of parasitization, host selection by *A. pseudococci* is a non-random process and other qualitative criteria, such as host stage (Islam & Copland, 1997) and previous parasitization are important. In a three-hour period of successive ovipositions, 2.5 times more frequent oviposition was recorded in unparasitized hosts than in parasitized hosts (table 1), indicating that *A. pseudococci* can distinguish between them. It must be borne in mind that in our experiments the parasitoids were unmated and therefore only able to produce male offspring. There appear to be no relevant studies on whether mating affects discrimination.

The frequency of rejection of parasitized hosts by *A. pseudococci* was significantly less at the beginning of a three-hour period of successive ovipositions, than towards the end (fig. 1), suggesting that the stimulus to oviposit was influenced by the ovarian egg-load. Van Lenteren (1981) has suggested that a strong ovarian pressure may inhibit the

Table 2. Mean percentage emergence of *Anagyrus pseudococci* from single parasitized and superparasitized *Planococcus citri*.

Host type (parasitized at different oviposition intervals)	Number of ovipositions	% emergence (n)
Singly parasitized (0–3 h)	108	67.6 (73)
Self-superparasitized (0–3 h)	43	74.4 (32)
Conspecific-superparasitized (0–3 h)	173	73.4 (127)
Conspecific-superparasitized (24–26 h)	50	74.0 (37)
Conspecific-superparasitized (48–50 h)	52	75.0 (39)
Conspecific-superparasitized (72–74 h)	47	72.3 (34)
Conspecific-superparasitized (96–98 h)	36	75.0 (27)

Percentage emergence in different host types is not significantly different (Chi-square test).

normal oviposition behaviour of parasitoids and cause some superparasitism. Females with low egg-loads are more likely to have their lifetime reproductive success constrained by the availability of eggs, and therefore would be predicted to select high quality hosts to maximize the fitness payoffs from the egg. Other reports on the acceptance of lower quality of hosts under higher egg-load conditions are those of Iwasa *et al*. (1984), Rosenheim & Rosen (1991) and Minkenberg *et al*. (1992). An alternative possibility would be that these successive oviposition patterns in *A. pseudococci* could be produced by changes in the perceptions of host availability but the specific experiments on egg-load would appear to refute this.

Vinson (1977) reported that host marking pheromones could reduce superparasitism. In the present studies the avoidance of parasitized hosts by parasitoids with both high and low egg-loads was high in newly (0–2 h) parasitized hosts, declined at 24–26 h and 48–50 h and then rose to a level similar to that of 0–2 h at 72–74 h and 96–98 h after parasitization (fig. 2). This biphasic discrimination was more profound when the parasitoids had low egg-loads. Although the assessment of a parasitoid's ability to discriminate is a complicated process (van Lenteren, 1981; van Alphen & Jervis, 1996), in the present study it was found that the females identified the parasitized hosts in two different ways, i.e. by antennal contact with the host (indicating detection of an external marker) and by ovipositor contact (which is considered to be a response to an internal marker). The former was more frequent in this study. The higher proportion of antennal rejection by *A. pseudococci* of hosts parasitized within the previous 48 h indicates that external cues or markers were probably left on the parasitized hosts and were detected by antennal encounter. The protruding stalk of the egg of the parasitoid or some chemicals deposited during oviposition would help identify the parasitized hosts.

Whilst the antennae play a role in the early stages of host discrimination, rejection can also occur during oviposition in hosts parasitized at intervals greater than 48 h. This indicates that the sensory receptors of the ovipositor are involved in detecting either the parasitoid eggs, the host's physiological condition or both (Wylie, 1965; Fisher, 1971). Parasitoid-induced biochemical changes have been observed in *P. citri* by *A. pseudococci* 24 and 48 h after parasitization (Islam *et al*., 1997). However, the present study suggests that the physiological changes in the hosts during the first 48 h (i.e. before the parasitoid eggs hatched) did not contribute to an increase in discrimination by the parasitoid. After about 72 h (i.e. after the parasitoid eggs had hatched in the mealybugs), the greater avoidance of parasitized hosts by *A. pseudococci* suggests a response to rapid parasitoid-induced changes in the host's physiology.

Although *A. pseudococci* showed a significant discrimination between parasitized and unparasitized hosts, the rate of oviposition was almost double in hosts parasitized by a conspecific-female than in the self-parasitized ones. Several authors have suggested that conspecific superparasitism could be profitable if there was a chance that her egg would develop into an adult by outcompeting the other larvae (van Alphen & Nell, 1982; Bakker *et al*., 1985; Hubbard *et al*., 1987; van Alphen & Visser, 1990).

Encapsulation of parasitoids is a common feature of mealybug parasitism and has been argued that it can increase the success of superparasitism. Blumberg *et al*. (1995) reported that 15.4% *P. citri* killed *A. pseudococci* through encapsulation. Oviposition in a parasitized host could be adaptive when encapsulation of the first egg laid in the host has exhausted or depleted the host's supply of haemocytes (Askew, 1968; van Alphen & Visser, 1990).

Superparasitism can be advantageous if younger larvae can destroy the older ones. Thus, conspecific superparasitism is thought to be an adaptive strategy for individual parasitoids when unparasitized hosts are rare (Charnov & Skinner, 1985; Hubbard *et al*., 1987; van Alphen & Visser, 1990). In a host-limited area, the ability of *A. pseudococci* to identify self- and conspecific-parasitized hosts would enable the female to maximize her fitness by ovipositing into conspecific-parasitized hosts and by avoiding hosts containing her own progeny. The mealybug parasitoid, *Apoanagyrus lopezi* De Santis (Hymenoptera: Encyrtidae), oviposits significantly more frequently in hosts parasitized by other females than in hosts parasitized by herself (van Alphen & Visser, 1990).

Supernumerary larvae may be eliminated by either physiological suppression or by physical combat. Van Baaren & Nenon (1996) determined the survival rate of parasitoid eggs deposited into already parasitized hosts by two encyrtid mealybug parasitoids. They found that the survival of the second larva was 10–30% and 7–23% in *A. lopezi* and *Leptomastix dactylopii* Howard (Hymenoptera: Encyrtidae) respectively, depending on the time interval between ovipositions. In *A. pseudococci*, if the younger larvae possess large mandibles, this may win the physical combat with the older ones.

The ability to avoid oviposition in previously parasitized mealybugs by parasitoids such as *A. pseudococci* is a desirable characteristic. The avoidance of superparasitism can reduce egg wastage and will therefore be a selective advantage (Rogers, 1975). However, in the present study, some superparasitism still occurred and indeed this could be advantageous if this avoided encapsulation or led to the second egg having a greater chance of survival. The degree of discrimination shown by *A. pseudococci* appears to be strongly related to the egg-load which influences the parasitoid's choice of whether to accept or reject a host it has already recognized as parasitized.

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Insecticide Resistance: From Mechanisms to Management

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Readership: Agricultural, medical and veterinary entomologists concerned with pest management. Resistance by insects and other arthropod pests to chemically-based control strategies is a major problem in crop protection as well as in medical and veterinary entomology. For every new approach to pest control, it seems that resistance is likely to develop.

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