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Field and Laboratory Observations on Oviposition by *Euploea core* (Insecta : Lepidoptera)

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Abstract

Oviposition behaviour of female *Euploea core* butterflies, a polyphagous species, was examined in the field and the laboratory. In the field females oviposited eggs singly on *Nerium oleander* and *Parsonsia straminea*. On *N. oleander* most eggs were laid on flowers and very young leaves. On *P. straminea* (none of which were flowering) very young leaves were favoured. In both species most eggs were laid on the undersurface of plant structures. Eggs tended to be located in the upper portions of plants, which reflects the general distribution of young foliage and flowers. This was more pronounced in *N. oleander* (a bush) than *P. straminea* (a vine). The distribution of eggs among both species was clumped. Height of *N. oleander* plants appeared to have no effect on oviposition, and neither did the distribution of plants. *N. oleander* plants in the shade were favoured above those in exposed positions. Plants of pink-, white- or red-flowered varieties were equally likely to be used. In the laboratory females oviposited on all plants offered from the families Asclepiadaceae, Apocynaceae and Moraceae, with *N. oleander* and *P. straminea* receiving many eggs. *Asclepias* species were sometimes highly favoured for oviposition, although these species are not suitable for larval development. No evidence was found for the prior presence or absence of eggs on plants influencing subsequent oviposition, nor was any evidence found for a marking pheromone influencing oviposition.

Introduction

Female butterflies display a wide range of host plant selection strategies, ranging from generalist to extreme specialist (Ehrlich and Raven 1965). A female must be able to locate habitats which contain suitable hosts (Sharpe *et al.* 1974; Wiklund and Ahrberg 1978; Rausher 1979). She must then locate plants within the habitat, and this will be influenced by her movement patterns (Jones 1977; McKay and Singer 1982; Zalucki and Kitching 1982*a*), and the density, dispersion and 'apparency' of the plants (Dethier 1959; Cromartie 1975; Jones 1977; Courtney 1982; Zalucki and Kitching 1982*b*). Having found a suitable host, she may decide to oviposit on the basis of plant characteristics which may be chemical (Dethier 1954, 1970; Fraenkel 1969; Feeny 1976; Chew 1977; Ives 1978; Stanton 1979), nutritional (Kennedy 1969; Chew 1975; Jones and Ives 1979), or possibly physical. The ability of a female to make these choices will be subject to genetic variation (Young 1979; Jaenike 1982), and the effects of learning (Rausher 1978), age and experience (Singer 1982; Zalucki and Kitching 1982*b*). Jaenike (1978) proposed that host selection is such that individual fitness is maximised, although there is no reason to assume that one optimum strategy exists for all females in a population (Fox and Morrow 1981; Wiklund 1981).

Euploea core corinna (W. S. Macleay) is a large nymphalid butterfly found throughout

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eastern and northern Australia (Kitching and Zalucki 1981). It is a polyphagous species, having been recorded from a wide range of native and exotic species in three plant families (Common and Waterhouse 1972; Scheermeyer and Zalucki 1985). In this paper we report the results of an investigation of oviposition by *E. core*. Firstly we describe the distribution of eggs in the field on two major species of host: one native, *Parsonsia straminea*, and the other introduced, *Nerium oleander*. Secondly, we present the results of laboratory experiments on host plant choice from a selection of the known and potential hosts of *E. core*. We also investigated the effect that eggs already present on host plants had on subsequent oviposition.

Materials and Methods

Field Observations

Nerium oleander ($n = 150$) were sampled for *E. core* eggs, between 5 and 19 January 1983, on the University of Queensland (UQ) campus (28°S.,152°E.) and in nearby suburbs. During the same period *Parsonsia straminea* ($n = 21$) were sampled from Griffith University (GU) campus (27°30′S.,153°E.) some 10 km south of UQ. For each plant 10 branches or vine lengths were sampled and their characteristics recorded (detailed in the results). Absence of eggs was presumed to be a result of absence of oviposition, although it may sometimes have been due to predation.

Laboratory Experiments

Experiments were performed in a glasshouse at the UQ campus, at a temperature range of 24–31°C. Butterflies were held in large flight cages made of metal framework covered with plastic mesh.

Butterflies. Three groups of *E. core* were used in the laboratory study: one consisted of adults collected from around the UQ campus; a second of adults emerging from pupae collected from *Nerium oleander* growing near UQ campus; and a third of adults collected near GU campus. These will be called the UQ group, the Oleander group and the GU group, respectively.

Butterflies had access to food from three sources: glass feeders, plastic containers with sponge wicks, and potted flowering non-host plants (*Lantana* sp. and *Pentis* sp.). The glass feeders were made by placing an oleander flower over the narrow end of a U-shaped pipette. Both the glass feeders and the plastic containers were filled with a 10% sucrose solution or water, and were suspended from the walls or ceiling of the cage.

Plants. The species of plants used are detailed in Table 2. All plants were grown in soil (standard UC mix) in plastic pots, and watered regularly. During the experimental periods only plants with fresh growth of leaves were used.

Experiment I: host plant preferences. Free-flying female *E. core* were offered a range of plant species (distributed randomly) on which to oviposit. Each morning eggs were counted and removed, plants were replaced, and the overall arrangement of plants altered. In 1983, ten females and four males from the UQ group were observed from 24 to 27 January, six females and three males from the oleander group were observed from 10 to 23 February, and four females and two males from the GU group were observed from 14 to 23 February. The groups of butterflies could not be tested simultaneously because butterflies or plants with fresh growth were sometimes unavailable.

Experiment II: effect of eggs on plants on subsequent oviposition. A pair of each plant species was placed in a cage, eight females and six males were released into it and were observed from 2 to 8 February 1983. Each morning eggs were counted, the positions of eggs on one plant of each pair were circled with a pen, and all the eggs were removed from the other plant.

Experiment III: oleander plants only. The effect of presence of eggs, egg contents, or possible marking pheromones was further investigated by allowing females ($n = 8$) to oviposit on two oleander plants, side by side, which were of similar size, shape, and condition. From 26 August to 1 September 1983, pairs of plants were used every second day, when treatments were reversed. Eggs were left on one plant and removed (i.e. flicked off) from the other. On another occasion (2–7 September) eggs were squashed on one plant, and on the other plant they were removed and the plant washed with distilled water. Again, treatments were reversed on alternate days. From 8 to 27 September, both parts of this experiment were repeated with plants set 1 m apart.

Results

Field Observations

Most of the 175 eggs were found as single eggs (per plant structure). Of 111 eggs on *N. oleander*, 90·1% were found as single eggs, 7·2% (8) in pairs and 2·7% (3) in a single group of three. Similarly, of 64 eggs from *P. straminea*, 82·8% were found as single eggs, 12·5% (8) in pairs and 4·7% (3) in a group of three. Eggs were found predominantly on the undersides of plant structures. The proportion of eggs on the undersurface was significantly different ($\chi_1^2 = 6{\cdot}33$, $P < 0{\cdot}02$) between the two species, being 59·5% on *N. oleander* and 78·2% on *P. straminea*, (leaves and stems only).

Table 1. Percentage of eggs found on parts of *Nerium oleander* and *Parsonsia straminea* plants

NA, not applicable or not available

Plant part	*Nerium oleander*		*Parsonsia straminea*	
	Mean size (cm)	Percentage eggs	Mean size (cm)	Percentage eggs
Leaves				
Very young	5	35·1	2	56·3
Young	7	5·4	5	21·9
Medium	9	3·6	9	10·9
Old	11	0·9	12	6·3
Flowers	NA	54·1	NA	—
Pods	NA	0·9	NA	—
Stem	NA	—	0·4[A]	4·7

[A] Stem thickness.

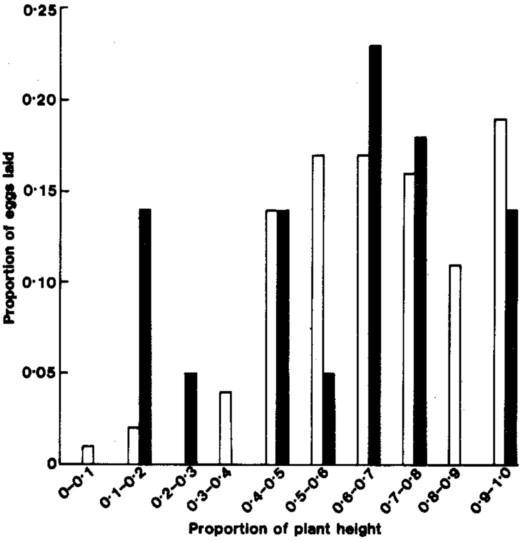

Fig. 1. Proportion of eggs laid plotted against the proportion of plant height above the ground at which they were laid. Open bars, *N. oleander*; solid bars, *P. straminea.*

Eggs were laid towards the top of plants of both host species (Fig. 1), mostly on very young leaves and flowers when available (Table 1). On *N. oleander* most eggs (89%) were oviposited on very young leaves and small flowers; no *P. straminea* were in flower during the sampling. Few eggs were found on the tougher-textured medium and old leaves of either species. *Nerium oleander* is a multistemmed plant, with young leaves and flowers usually towards the top of each stem (although the distribution of eggs may in part be due to more of the plant being higher above the ground); fresh growth of leaves or shoots lower down a plant may also receive eggs. *Parsonsia straminea* is a vine; tendrils with fresh leaves often hang down, so that subsequently a higher proportion of eggs is found 'lower' down the plant (Fig. 1).

The distribution of eggs among *N. oleander* and *P. straminea* plants was clumped (Fig. 2). The index of dispersion (Southwood 1978) for eggs on *N. oleander* plants was 1071·19 (149 d.f., $P<0·001$) indicating a high degree of clumping. Most *N. oleander* plants received no eggs or only one; however, six plants accounted for over half of the eggs recorded, with 5, 5, 9, 12, 16, 16 eggs per plant (these plants were not all growing together). The index of dispersion for eggs on *P. straminea* was 48·16 (20 d.f., $P<0·001$), also indicating a high degree of clumping.

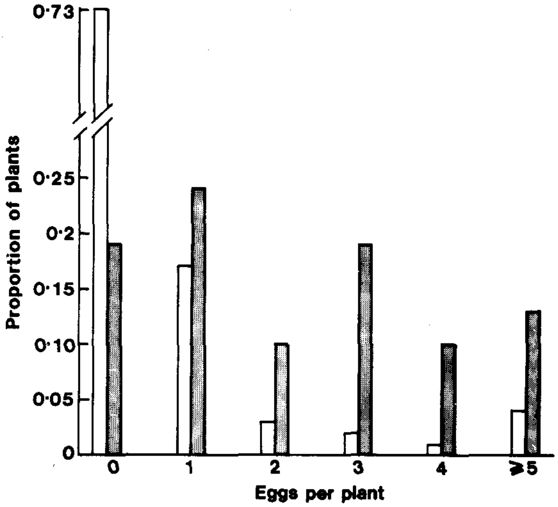

Fig. 2. Frequency distribution of eggs per plant found on *N. oleander* (open bars) and *P. straminea* (solid bars).

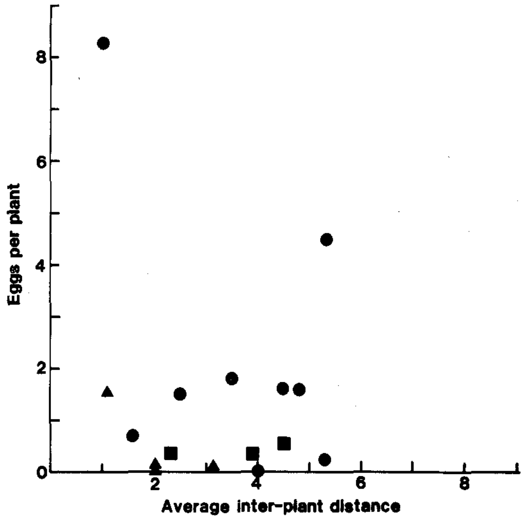

Fig. 3. Effect of patchiness (average interplant distance) on the number of eggs per plant on *N. oleander*. Symbols refer to number of plants in a group: ● 2–5; ■ 6–9; ▲ 10–13.

For oleander plants with at least one egg there was no relationship between plant height and number of eggs ($r=0·071$, $n=40$; $P>0·10$). There was also no indication that variation in flowering or growth status of plants contributed to this result. At the time of sampling all *N. oleander* were flowering and had growth of new leaves. There were no small plants or recently pruned plants in the sample, and this may be why no plant size effect was detected.

As *P. straminea* are vines, which were either growing on trees or spreading on the ground, a simple measure of size was not possible.

The *N. oleander* sampled were growing singly or, usually, in rows. There were no eggs on single plants ($n = 7$). No relationship was detected between the number of eggs per plant and the average distance between plants in a group ($r = -0{\cdot}134$, $n = 17$, NS), nor between the number of eggs per plant and the number of plants in a group ($r = -0{\cdot}309$, $n = 17$, NS) (see Fig. 3).

The effect of plant location (shade or exposed) and variety (based on flower colour of *N. oleander* only) on oviposition was examined by means of χ^2 analysis. We compared numbers of plants with and without eggs rather than total numbers of eggs in the various categories, because egg distribution was clumped (see above). Plants in the open were less likely ($\chi_1^2 = 50{\cdot}03$; $P < 0{\cdot}001$) to be oviposited on than plants in the shade; 26 of 37 plants in the shade and 13 of 113 in the open had eggs laid on them. Plants of each variety were equally likely ($\chi_2^2 = 1{\cdot}21$, NS) to be oviposited on; 5 of 28 white-flowered plants, 29 of 103 pink-flowered plants, and 5 of 19 red-flowered plants were laid on. The effect of plant location on oviposition on *P. straminea* could not be tested, because all the plants were growing in a forest habitat and were shaded.

Table 2. Total numbers of eggs laid on various plants by groups of *E. core* females (experiment 1)

UQ, University of Queensland; GU, Griffith University

Family and species of host plant	Adults from UQ	Adults from pupae on *N. oleander*	Adults from GU
Asclepiadaceae			
Asclepias fruticosa	39	54	52
Asclepias curassavica	92	2	6
Hoya australis	5	0	0
Stephanotis sp.	25	13	2
Cryptostegia sp.	49	6	0
Calotropis sp.	–	0	2
Apocynaceae			
Nerium oleander	65	85	16
Parsonsia straminea	50	16	47
Parsonsia phaseophylla	0	1	–
Moraceae			
Ficus obliqua	6	6	5
Ficus benjamina	3	–	4

Laboratory Experiments

Experiment I. The results of this experiment are summarised in Table 2. Since the range of host plants offered to each butterfly group differed slightly, an analysis comparing groups was not possible. Each group was analysed separately by the Friedman non-parametric test (Lehmann 1975), each day being treated as a block. The tests showed that plant species were not utilised similarly by ovipositing females. The value of Q for the UQ, Oleander and GU groups was $21{\cdot}00$ ($P < 0{\cdot}05$), $27{\cdot}46$ ($P < 0{\cdot}01$), and $21{\cdot}24$ ($P < 0{\cdot}05$) respectively (each with nine degrees of freedom). All of the species offered were laid on at some stage. The results were not consistent across groups, although *N. oleander* and *P. straminea* generally received many eggs. *Asclepias fruticosa* received many eggs in all three groups, but *A. curassavica* received many eggs in the UQ group only.

Experiment II. The mean number (± SE) of eggs laid on plants already with eggs versus the number on plants without eggs for each of the three days of the experiment was:

1·38 ± 1·30 ($n=8$) *v.* 0·63 ± 0·74 ($n=8$), 1·90 ± 1·85 ($n=10$) *v.* 1·60 ± 1·90 ($n=10$) and 4·70 ± 4 ($n=10$) *v.* 3·5 ± 2·55 ($n=10$). Plants with eggs consistently received a higher number of eggs than plants without eggs (1·57 times as many, averaged over three days), but the differences between treatments on any one day were not significant (t-test on $\log(x+1)$ transform of number of eggs laid on each plant: $t=1\cdot27$, 0·26, 0·08 for the three days respectively). Because we did not reverse treatments with respect to plants, any effect could be due to either the plants or a marking pheromone, or the presence of eggs *per se*. We further tested these effects in experiment III (below).

Table 3. The effects on oviposition of eggs already laid on the host plant

Arrows indicate movement of plants between days. Values in parentheses are the numbers of eggs left on plants. ANOVA analysis: NP, number of eggs on previous day

Day No.	Plants 1 m apart With eggs	Plants 1 m apart Without eggs	Plants touching With eggs	Plants touching Without eggs
1	(12) 5	5	(12) 14	10
2	(4) 4	5	(9) 12	13
3	(5) 5	13	(10) 12	16
4	(5) 16	14	(13) 34	14
5	(13) 7	7	(16) 9	6
6	(14) 8	6	(14) 4	13
7	(7) 3	2	(6) 13	15
8	(6) 3	6	(13) 23	13
9	(2) 7	4	(15) 16	9
10	(5) 7	10	(13) 15	22
11	(4) 4	6	(9) 2	4
12	(10) 9	21	(22) 8	5
13	(6) 5	2	–	–
14	(21) 19	7	–	–
15	(1) 11	1	–	–
16	(7) 4	4	–	–
17	(1) 7	1	–	–
18	(4) 7	8	–	–

Source	D.F.	Adjusted mean square	Sig.	D.F.	Adjusted mean square	Sig.
Plant	3	0·394	NS	3	0·532	$P<0\cdot05$
Treatment	1	0·041	NS	1	0·0013	NS
Times	16	0·431	NS	10	0·487	$P<0\cdot05$
Log NP	1	0·257	NS	1	0·054	NS
Residual	14	0·1196		8	0·036	

Experiment III. Tables 3 and 4 show the numbers of eggs laid each day on oleander plants already with eggs and on those without eggs, and the numbers on plants where eggs had been squashed compared with those on plants where eggs had been removed and leaves washed thoroughly with distilled water. This experiment was performed with pairs of plants either side by side or 1 m apart. If there is a marking pheromone, the distance between plants may influence our results. During the experiment plants in one treatment were placed into the other treatment on alternate days, thus removing any effect of plant condition from the results (see Tables 3 and 4 for details).

An analysis of variance for unbalanced data (made with the GLIM statistical package) was performed on the $\log(x+1)$ transform of the number of eggs per plant in each of the treatment categories. In the two experiments in which the effects on oviposition of plants with and without eggs were compared we could not detect a treatment effect (if all the other factors are included) ($P>0\cdot 05$, Table 3). In the repeat of this experiment, when plants were touching (Table 3), there was a significant effect of plant ($P<0\cdot 05$) and time ($P<0\cdot 05$) on oviposition, the former possibly indicating a response to plant quality and the latter the decline in egg-laying over the course of the experiment. The 'squash' versus 'remove and wash' treatments are detailed in Table 4. Again there was no effect of treatment on egg-laying (when all other factors are included in the analysis). In the experiment with plants touching (Table 4) there was a slight effect of plant, and possibly of (log) number of eggs on the plant on the previous day. We can conclude that the methods outlined above cannot demonstrate any effect of eggs enhancing or pheromones deterring oviposition.

Table 4. The effects on oviposition of possible pheromones from previously laid eggs on host plant

Conventions as in Table 3

Day No.	Plants 1 m apart: Eggs squashed	Plants 1 m apart: Eggs removed, plant washed	Plants touching: Eggs squashed	Plants touching: Eggs removed, plant washed
1	4	9	7	14
2	6	6	8	14
3	24	7	18	4
4	17	15	19	12
5	9	11	13	13
6	11	7	14	18
7	3	4	9	10
8	6	2	12	26
9	2	12	13	14
10	3	4	14	16
11	–	–	18	13
12	–	–	26	14

Source	D.F.	Adjusted mean square	Sig.	D.F.	Adjusted mean square	Sig.
Plant	1	0·122	NS	1	0·440	$P<0\cdot 1$
Treatment	1	0·103	NS	1	0·0003	NS
Times	8	0·366	NS	10	0·129	NS
Log NP	1	0·090	NS	1	0·421	$P<0\cdot 1$
Residual	6	0·325		8	0·122	

Discussion

The eggs of *Euploea core corinna* are relatively large (mean height ±SD, $1\cdot 77\pm 0\cdot 28$ mm, $n=175$, width *c.* $0\cdot 60$ mm) and females show considerable selectivity of sites for oviposition. Most eggs were laid singly and on the undersurface of plant parts of field-sampled *N. oleander* and *P. straminea*. Rarely was more than one egg found on the same plant structure, except as the outcome of more than one oviposition. This could be inferred from the change in colour of the eggs as they aged.

Euploea tended to oviposit on plant parts towards the top of the two host species sampled. Actively growing plant parts received more eggs than older ones. Actively growing parts are usually soft, have concentrations of allelochemicals different from those in other parts, and are probably higher in nutrients. These factors will influence the survival and growth of early larval instars (e.g. Barbosa and Greenblatt 1979); in particular, early instars of *E. core* larvae have difficulty biting through the tough-textured mature leaves (Zalucki, unpublished observations). Oviposition on flowers is either a response to their position on *N. oleander* or indicates a definite preference for flowers; the large number of eggs on *N. oleander* flowers suggests the latter. In laboratory experiments eggs were laid on artificial feeders which contained fresh oleander flowers, and in the field larvae have been observed eating the flower buds of *N. oleander* (Zalucki, unpublished observation).

Female *E. core* lay their eggs singly, as do most butterfly species (Stamp 1980), but in the field the distribution of eggs was clumped. The dispersion of *Euploea* host plants did not seem to affect the number of eggs a plant would receive; however, *N. oleander* plants in shaded areas were more likely to receive eggs than those in open areas. This type of effect on oviposition (viz. shaded *v*. exposed plants) has been noted in other Lepidoptera (see Rausher 1979; McKay and Singer 1982) and plant quality and texture have been implicated (Ives 1978; Myers *et al.* 1981). The preference for shaded plants may also reflect a preference by adults for searching in shaded habitats. The proportion of plants, in each of the three varieties (white-, red- and pink-flowered) of *N. oleander* sampled, that received eggs, was the same.

Assessment of eggs by female butterflies has been reported by several authors (Rothschild and Schoonhoven 1977; Dixon *et al.* 1978; Rausher 1979; Shapiro 1981; Williams and Gilbert 1981). Dixon *et al.* (1978) reported that *Euploea core amymone* oviposited on *N. oleander* already bearing eggs. This is the only butterfly for which the presence of eggs on plants is reported to make them more attractive for oviposition, and could explain the clumped pattern of oviposition we found on *N. oleander* and *P. straminea* in the field. However, in our laboratory experiments we found no evidence for an effect of eggs or a marking pheromone on subsequent oviposition.

Choice of host species may also influence the survival and development of a female's offspring. *Euploea core* is a polyphage which has been recorded from a wide range of native and exotic plants in the families Asclepiadaceae, Apocynaceae and Moraceae (Scheermeyer and Zalucki 1985). It is not surprising to find that females oviposited on all the plant species offered in the laboratory. However, not all plants were treated equally. Interestingly, species of *Asclepias* were among those preferred for oviposition by all experimental groups of butterflies. These plants are unsuitable for larval development (Kitching and Zalucki 1981; Rahman *et al.* 1985), but *E. core* eggs have been found on *Asclepias* species in the field (Kitching and Zalucki 1983). Relative to the other plant species presented, *Asclepias* spp. have softer-textured leaves and may appear to an ovipositing female to be more nutritionally suitable. Presumably they also have the chemical cues shared with other members of the family Asclepiadaceae, within which *Euploea* has many native and exotic hosts (although note *Calotropis* and *Hoya* were largely ignored). Nevertheless females which chose *Asclepias* species had made a 'mistake' in terms of maximising fitness. Similar ovipositional mistakes have been reported for several other butterfly species (Wiklund 1975; Chew 1977, 1980; Courtney 1981).

Whatever the cues, *Euploea* oviposit on a wide range of hosts, including plants which contain milky latex (e.g. native *Ficus*, exotic *Asclepias*, *Nerium*, *Cryptostegia* and *Hoya*). In the Brisbane region they also oviposit and successfully develop on *Ficus benjamina* (Rahman *et al.* 1985), an exotic Moraceae not recorded as a host by Common and Waterhouse (1972). Chew (1975) points out that species which lay eggs singly and visit many different host plants may be slow to evolve consistent species preferences. However, there would be strong selection pressure for discrimination between plants within species, since a plant which was poor for larval development (e.g. due to water stress or low nutrients) would be much the same across plant species (Jones and Ives 1979). In *E. core*, expansion of host range to include exotics appears to be the result of a change in the ability of larvae to develop and survive on plants which are often sampled by ovipositing females.

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