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Larval performance on and oviposition preference for known and potential hosts by *Lobesia botrana* (Lepidoptera: Tortricidae)

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Tortricidae, *Lobesia botrana*, host-plant suitability, oviposition preference

Abstract. Ex ovo larvae of *Lobesia botrana* were reared on flowers and fruits of known and potential host plants, both in the laboratory and in the field. Development rates indicated a wide range of host suitability. In the laboratory, larvae of *L. botrana* had higher survivorship and shorter development time when reared on *Vitis vinifera*, *Prunus persica* (*nectarina*), *Taraxacum officinale* or *Prunus domestica* than when reared on *Malus pumila*, *Pyrus amygdaliformis*, *Prunus armeniaca*, *Prunus cerasus*, *Syringa vulgaris* or *Papaver rhoeas*. Similar results were obtained in the field. In no-choice tests in the laboratory, more eggs were laid on fruits than on flowers. Fruits of *Prunus domestica*, *Vitis vinifera* and *Prunus persica* (*nectarina*) were most preferred as oviposition sites.

INTRODUCTION

The grape berry moth *Lobesia botrana* (Denis & Schiffermueller) (Lepidoptera: Tortricidae) is the major pest in vineyards of southern Europe. Larvae of the first generation damage the inflorescences, and those of following two or three generations damage the green, ripening and ripe berries. *L. botrana* is a polyphagous species, with reported host plants belonging to 27 plant families, including Vitaceae, Thymelaeaceae, Rosaceae, Oleaceae, Ranunculaceae, Polygonaceae, Apiaceae, Asteraceae, Convolvulaceae and Rhamnaceae (Balachowsky & Mesnil, 1935; Bovey, 1966; Galet, 1982; Stoeva, 1982; Roditakis, 1989; Moleas, 1988). *Daphne gnidium* (Thymelaeaceae) appears to constitute the ancestral host of *L. botrana* (Balachowsky & Mesnil, 1935). Frequent utilization of the grape [*Vitis vinifera* (Vitaceae)] as host is considered to be relatively recent, because the insect was rare in the vineyards of France until the early 1930s (Balachowsky & Mesnil, 1935). Oleaceae hosts include the cultivated olive, *Olea europaea* L. and the ornamental plants *Syringa vulgaris* L. and *Ligustrum vulgare* L. (Balachowsky & Mesnil, 1935; Bovey, 1966; Stoeva, 1982). Generally, the species is considered to be polyphagous, and both inflorescences and fruits may be commonly fed upon. Tzanakakis & Savopoulou (1973) reported that larvae of *L. botrana* were found on inflorescences of olive trees near an abandoned vineyard in Halkidiki (northern Greece). In Bulgaria, Stoeva (1982) observed that up to 45% of olive flowers were infested by first generation larvae. She also found the pupal length, pupal weight and adult fecundity of field-collected *L. botrana* to be greater in the larvae fed on olive inflorescences compared with those fed on vine inflorescences or sweet cherry fruits. It has been found that olive inflorescences supported larval growth equally well as grape flowers (Savopoulou-Soultani & Tzanakakis, 1989; Savopoulou-Soultani et al., 1990).

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The adults are active in spring about 1–1.5 month before *V. vinifera* flowers are present. Furthermore, females are active 2–3 months after the harvest of precocious grapes. To clarify the possible role of alternate hosts as reservoirs, common wild and cultivated plants were tested for their suitability as food for the larvae and also as oviposition substrates.

MATERIAL AND METHODS

Insects

The larvae used originated from our laboratory culture maintained on an artificial diet for 5 generations, using methods described earlier (Tzanakakis & Savopoulou, 1973; Savopoulou-Soultani & Tzanakakis, 1979; Savopoulou-Soultani et al., 1994).

Host plants tested

Larvae were reared on flowers of plants which blossom earlier than *Vitis vinifera* (Vitaceae) and/or on fruits of some plant species, such as the wild plants *Taraxacum officinale* Web., *Onopordum* sp. and *Chamomilla recutita* L. (Compositae), *Lamium amplexicaule* L. (Labiatae), *Papaver rhoeas* L. (Papaveraceae), *Rubus fruticosus* L. and *Pyrus amygdaliformis* Vill. (Rosaceae); the ornamentals, *Syringa vulgaris* L. (Oleaceae), *Nerium oleander* L. (Apocynaceae); and the cultivated plants *Prunus cerasus* L., *P. persica nectarina* L., *P. armeniaca* L., *P. domestica* L. and *Malus pumila* Mill. (Rosaceae). Five out of these (*V. vinifera, S. vulgaris, T. officinale, L. amplexicaule*, and *P. cerasus*) have been previously reported as hosts for *L. botrana* (Balachowsky & Mesnil, 1935; Bovey, 1966). All the above plants were grown in the University Farm, near Thessaloniki.

The plant parts were collected about 20 days after the first male from the overwintering generation (April-May for flowers) or from the first generation (June-July for fruits) was caught in a pheromone trap.

Laboratory experiments

One detached flower or inflorescence with a piece of moist cotton at the base of its axis was placed in a 9 cm diameter glass Petri dish, while each fruit was placed in a transparent plastic cup. Ten ex ovo larvae were placed in each Petri dish or plastic cup, and larval development was monitored daily. Withered or rotten plant parts were promptly replaced. Rearing conditions were 16L : 8D and 25 : 23°C. A piece of corrugated paper was provided for pupation. Pupae were maintained under the same conditions as larvae and weighed when 7–10 days old.

Duration of larval development, pupal weight and percentage of survival until adulthood were recorded.

Field experiments

Ten newly hatched larvae were placed on the apical part of a twig bearing 4 inflorescences or flowers (in spring) or fruits (in summer) and enclosed within an organdie bag. To assure that larvae would feed only on flowers or fruits, leaves were removed. When herbaceous plant species were used, the whole plant with 10 larvae was caged in an organdie bag. Each host was checked by 5 replicates. The larval stage and the condition of the inflorescences or fruits were checked twice a week. The pupae were transferred to laboratory conditions given above and weighed when 7–10 days old.

Oviposition preference

Experiments were conducted in the laboratory at 16L : 8D and 25 : 23°C. The moths were held in groups of 5 pairs in plastic cups as described by Savopoulou-Soultani et al. (1994) until tested. Mated females were transferred into 15 × 15 × 15 cm cages on the day following the first oviposition. Three females placed together in a cage with one flower or inflorescence (in spring) or fruit (in summer) constituted a replicate. There were 7 replicates per treatment. After one day the eggs laid were counted.

Statistical analysis

Development time and pupal mass were analysed by ANOVA. If F-tests were significant, then PLSD tests were used for separation of means at a probability level of 0.05 (Stat View II 1988, Version 1.03, Abacus Concepts, Inc.). The percentages of survival were compared using χ^2-analysis (contingency tables calculated on original counts).

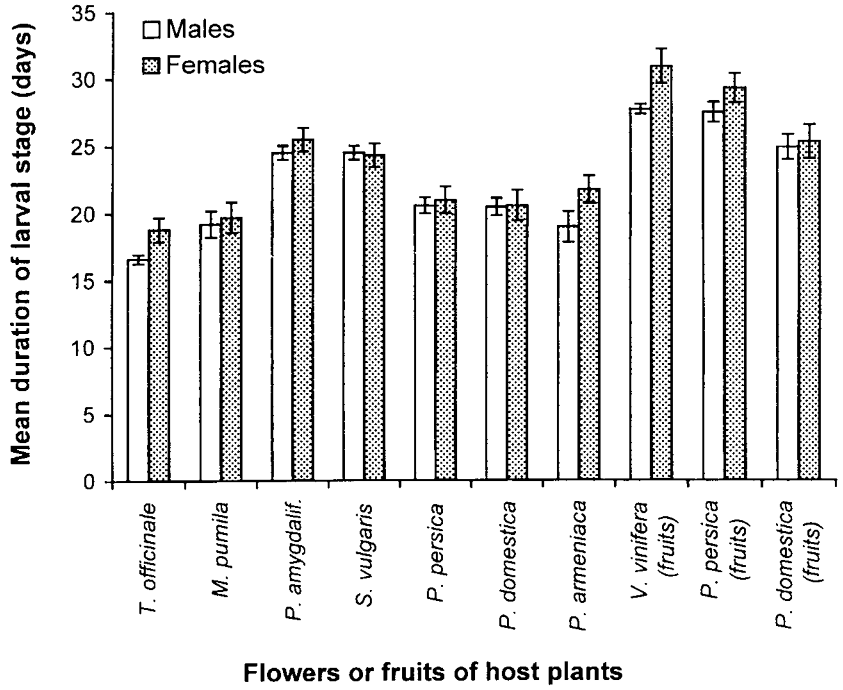

Fig. 1. Mean duration of larval stage (± S.E.) of *L. botrana* on different host plant flowers and fruits in the laboratory.

RESULTS

Larval development

SPRING EXPERIMENT IN THE LABORATORY. Male larvae developed faster when reared on flowers of *T. officinale* than when reared on all the other hosts ($F = 14.13$, $df = 6, 28$, $P < 0.001$) (Fig. 1). This was also true for larval development of females ($F = 5.75$, $df = 6, 28$, $P < 0.001$), although development time on *T. officinale* was not significantly different from that on *M. pumila*, *P. domestica* or *P. persica* (*nectarina*). Both male and female larvae had the longest development time when reared on *S. vulgaris* and *P. amygdaliformis* flowers. No larvae completed the development successfully when reared on *N. oleander*, *L. amplexicaule*, *C. recutita* and *Onopordum* sp. and only very few larvae pupated when reared on *P. cerasus* and *P. rhoeas*. The last mentioned plants are not included in this and subsequent figures.

SUMMER EXPERIMENT IN THE LABORATORY. Both male and female larvae had shorter development time, when reared on *P. domestica*, than those reared on *V. vinifera* and fruits of *P. persica* (*nectarina*) ($F = 4.57$, $df = 2, 12$, $P < 0.05$ and $F = 5.52$, $df = 2, 12$, $P < 0.05$ respectively; Fig. 1). All larvae reared on *S. vulgaris* and *R. fruticosus* died when in the 2nd or 3rd instar, and only a few larvae pupated successfully when reared on fruits of *P. amygdaliformis*, *M. pumila* and *P. armeniaca* (the last mentioned plants are not included in the figures).

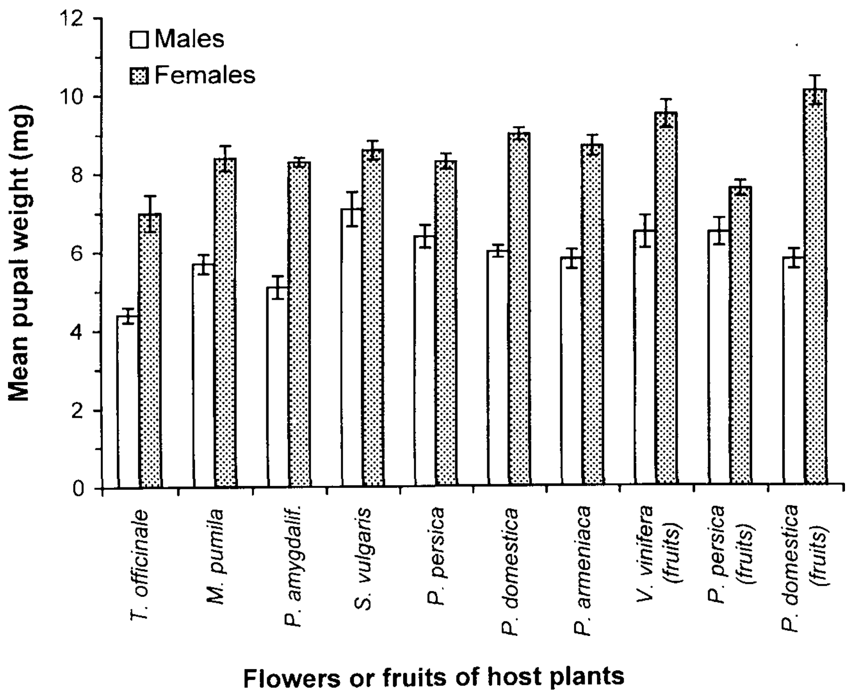

Fig. 2. Mean pupal weight (± S.E.) of *L. botrana* reared on different host plant flowers and fruits in the laboratory.

Spring experiment in the field. Male larvae exhibited shorter development time when reared on flowers of *P. persica* (*nectarina*) than those reared on *T. officinale* and *P. domestica* ($F = 28.29$, $df = 2, 12$, $P < 0.001$; Table 1). When reared on other plants, no larvae or only very few of them completed their development successfully. The same was observed with female larvae (not included in the table).

Table 1. Duration of larval stage and pupal weight on flowers and fruits in the field in males of *Lobesia botrana*. Within each experiment and column, the numbers followed by the same letter do not differ significantly at the 0.05 level, by PLSD test.

Larval diet	Duration (in days) (mean ± S.E.)	Pupal weight (mg) (mean ± S.E.)
Flowers		
Taraxacum officinale	44.3 ± 0.8b	4.9 ± 0.2a
Prunus persica (*nectarina*)	40.2 ± 1.3a	6.0 ± 0.6b
Prunus domestica	51.8 ± 1.2c	5.8 ± 0.3b
Fruits		
Vitis vinifera	44.2 ± 1.5a	4.9 ± 0.2a
Prunus domestica	51.8 ± 1.7b	5.6 ± 0.3a

Summer experiment in the field. Faster development was observed in the male larvae reared on *V. vinifera* than those reared on *P. domestica* fruits ($F = 11.15$, $df = 1, 8$, $P <$

0.05; Table 1). On the other plants, no male larvae or only a few completed their development successfully. The same was observed with female larvae on all plants, so they are not included in the table.

Pupal weight

SPRING EXPERIMENT IN THE LABORATORY. Males feeding on flowers of *S. vulgaris* produced the heaviest pupae ($F = 9.74$, $df = 6, 28$, $P < 0.001$), although their mass was not significantly different from the mass of pupae that had fed on flowers of *P. persica* (*nectarina*) during the larval stage (Fig. 2). The lightest pupae (both male and female) were those fed on flowers of *T. officinale* during the larval stage ($F = 5.51$, $df = 6, 28$, $P < 0.001$ in females). Their mass was significantly different from pupae reared on all the other flowers.

SUMMER EXPERIMENT IN THE LABORATORY. We observed no significant differences in the pupal mass among any of the treatments for males ($F = 1.34$, $df = 2, 12$, $P > 0.05$), while the female larvae fed on fruits of *V. vinifera* and *P. domestica* produced heavier pupae ($F = 17.32$, $df = 2, 12$, $P < 0.001$; Fig. 2) than on *P. persica*.

SPRING EXPERIMENT IN THE FIELD. The male pupae reared on flowers of *T. officinale* were the lightest and they differed significantly from the pupae reared on *P. persica* (*nectarina*) and *P. domestica* ($F = 4.58$, $df = 2, 12$, $P < 0.05$; Table 1).

SUMMER EXPERIMENT IN THE FIELD. The same was observed with pupal weight in the field (Table 1), except that on *P. persica* (*nectarina*) only a few larvae successfully pupated ($F = 4.08$, $df = 1, 8$, $P > 0.05$).

TABLE 2. Survival to imago of *Lobesia botrana* reared on known and potential hosts, 5×10 ex ovo larvae per treatment. Within each experiment and column, the numbers followed by the same letter do not differ significantly at the 0.05 level, by χ^2-criterion (the percentages calculated from the analysed raw data).

Larval diet	Adults as percentage of L1 and pupae			
	In the laboratory		In the field	
	L1	Pupae	L1	Pupae
Flowers				
Taraxacum officinale	34.0ab	100.0a	8.0a	44.4a
Malus pumila	28.0abc	82.4ab	4.0a	66.7a
Prunus cerasus	8.0c	66.7b	2.0a	33.3a
Papaver rhoeas	12.0bc	66.7b	0.0	0.0
Pyrus amygdaliformis	26.0abc	92.9ab	6.0a	50.0a
Syringa vulgaris	26.0abc	86.7ab	0.0	0.0
Prunus persica (*nectarina*)	30.0abc	68.2b	12.0a	85.7a
Prunus domestica	32.0ab	76.2ab	10.0a	62.5a
Prunus armeniaca	24.0abc	66.7b	4.0a	33.3a
Fruits				
Vitis vinifera	30.0a	78.9a	24.0a	80.0a
Prunus persica (*nectarina*)	24.0a	80.0a	6.0bc	50.0a
Prunus domestica	16.0ab	61.6ab	14.0a	77.8a
Prunus armeniaca	4.0b	25.0b	2.0c	33.3a
Malus pumila	6.0b	50.0ab	4.0bc	66.7a
Pyrus amygdaliformis	4.0b	50.0ab	4.0bc	33.3a

Survival

SPRING EXPERIMENT IN THE LABORATORY. Larval survival on flowers varied from 8% to 34% (Table 2), the only significant difference occurring between *T. officinale* and *P. domestica* against *P. cerasus* ($\chi^2 = 4.34$ and $\chi^2 = 4.12$ respectively, df = 1, P < 0.05). Pupal survival varied between 66 and 100%. The survival was the highest when larvae were reared on *T. officinale*. However, the differences between the survival of pupae on *P. amygdaliformis*, *S. vulgaris*, *M. pumila*, *P. domestica* and *T. officinale* were not significant ($\chi^2 = 1.25$, $\chi^2 = 2.48$, $\chi^2 = 3.29$ and $\chi^2 = 3.81$ respectively, df = 1, P > 0.05). The larval survival was generally low.

SPRING EXPERIMENT IN THE FIELD. The larval survival was generally low with no significant differences observed among hosts. There were no differences in the pupal survival among the hosts, either. No larvae survived on *L. amplexicaule*, *C. recutita*, *N. oleander* and *Onopordum* sp. so they are not included in the table.

SUMMER EXPERIMENT IN THE LABORATORY. While the larval survival was greatest on the fruits of *V. vinifera*, it did not significantly differ from survival of larvae reared on *P. persica* (*nectarina*) and *P. domestica* ($\chi^2 = 2.33$ and $\chi^2 = 3.12$ respectively, df = 1, P > 0.05; Table 2). No larvae survived on fruits of *R. fruticosus* and *S. vulgaris*. The survival of pupae reared on *V. vinifera* and *P. persica* (*nectarina*) was significantly different from the survival on *P. armeniaca* ($\chi^2 = 6.62$ and $\chi^2 = 7.03$ respectively, df = 1, P < 0.05).

SUMMER EXPERIMENT IN THE FIELD. The larval survival was greatest among larvae reared on fruits of *V. vinifera*. However, survival on this host did not significantly differ from that on *P. domestica* ($\chi^2 = 3.43$, df = 1, P > 0.05). The pupal survival was generally high without significant differences among the host fruits.

TABLE 3. Oviposition by *Lobesia botrana* on known and potential hosts in no-choice test.

Oviposition substrate	Mean no. eggs / replicate / day[1]	
	Flowers	Fruits
Vitis vinifera	–	30.8a[2]
Prunus cerasus	3.0a	–
Prunus persica (*nectarina*)	2.7ab	29.1a
Prunus domestica	2.3abc	32.0a
Prunus armeniaca	2.0abcd	15.1c
Papaver rhoeas	1.9abcde	–
Pyrus amigdaliformis	1.1cdef	18.4bc
Syringa vulgaris	1.0cdef	0.7d
Lamium amplexicaule	0.7def	–
Chamomilla recutita	0.6ef	–
Malus pumila	0.6ef	20.1b
Nerium oleander	0.6ef	–
Onopordum sp.	0.4f	–
Taraxacum officinale	0.4f	–
Rubus fruticosus	–	4.8d

[1] 3 females were used in a replicate.
[2] Within each experiment and column, means followed by the same letter do not differ significantly at the 0.05 level, by PLSD test.

Oviposition preference

THE FLOWERS. As seen in Table 3, the highest number of eggs was laid on flowers of *P. cerasus* ($F = 3.53$, $df = 12, 98$, $P < 0.01$), although the number was not significantly different from the number laid on flowers of *P. persica (nectarina)*, *P. domestica*, *P. armeniaca* and *P. rhoeas*. No eggs were laid on *R. fruticosus*. In all cases, some eggs were observed on the sides of the plastic bottles containing the flowers tested.

THE FRUITS. The number of eggs laid on fruits of *V. vinifera*, *P. persica (nectarina)* and *P. domestica* was higher than on the fruits of other species ($F = 65.64$ $df = 7, 56$, $P < 0.01$).

DISCUSSION

Both the laboratory and field experiments demonstrate that *L. botrana* is capable of development on several potential wild or cultivated host plants commonly found adjacent to the vineyards. *P. persica (nectarina)*, *P. domestica* and *T. officinale* all have the potential to serve as reservoirs for populations of *L. botrana*, especially early in spring, as they bloom earlier than *V. vinifera*. Females are active about a month before the blooming of *V. vinifera* and may, thus, lay some or all their eggs on alternative host plants, such as olive, found adjacent to the vineyards (Savopoulou-Soultani et al., 1990). We observed that *L. botrana* larvae develop as well, or even better, on plants such as *Olea europaea* (Savopoulou-Soultani & Tzanakakis, 1989; Savopoulou-Soultani et al., 1990) than on *V. vinifera*, which is a regular host in the field. This is true for some other herbivorous insects too (Thompson, 1988). Thus, the alteration in host plants may have importance for the evolution of insect diet breadths (Fox & Lalonde, 1993). It is already known that *L. botrana* moved to orchards of the kiwi tree (*Actinidia chinensis*) in the Bari region of Italy when grape was removed (Moleas, 1988). The present results suggest that peach and plum groves could contribute to the production of large numbers of first generation adults and constitute an important and unanticipated source of grape vine infestations. Wild malvaceous plants have been reported to be important early-season or late-season hosts of other insects too, such as *Helicoverpa zea* and *Heliothis virescens* (Sudbrink & Grant, 1995).

Although there were significant differences among the development time on different hosts, these differences may indicate a range of host suitability rather than host/non-host relationships. The plants which had been previously described as known hosts of *L. botrana*, most notably *S. vulgaris*, *L. amplexicaule* and *P. cerasus*, were less suitable for larval development than several potential hosts tested. Other potential host plants may also play a significant role in the maintenance of this insect in areas where precocious grape varieties are cultivated. In these areas, males were caught in pheromone traps up to several weeks after grapes were harvested in August. This suggests that the females of the third generation may oviposit and the larvae may develop on alternative host plants.

The larvae were not capable to survive on *L. amplexicaule*, *C. recutita*, *N. oleander*, *Onopordum* sp. and *R. fruticosus*, possibly due to the presence of toxins, feeding and/or oviposition deterrents in the plants.

Pupal weight and fecundity are positively correlated in *L. botrana* (unpublished data). Consequently, fecundity of females produced from larvae reared on host plants other than *V. vinifera*, could be as high as the fecundity of larvae reared on *V. vinifera*.

Oviposition on unsuitable hosts will reduce offspring survival. In some species, the females do not discriminate well the oviposition sites and may lay eggs on hosts of reduced suitability for larval development, in order to maximize their own fecundity (Jaenike, 1990).

Generally, more eggs were laid on fruits than on flowers, especially in *P. domestica*, *V. vinifera* and *P. persica (nectarina)*. However, larval development was generally shorter on flowers than on fruits, both in the field and in the laboratory.

Provided that females in the field recognize the potential hosts tested here as oviposition sites, the study suggests that host-range expansion of *L. botrana* to *P. domestica* and *P. persica* (*nectarina*) is possible. Predictions about the course of this expansion would require more information about oviposition preference and genetic variation in performance.

The short development time and high survival rate of larvae, coupled with the high number of eggs laid on *P. persica* (*nectarina*) and *P. domestica*, suggest that these host plants may be as suitable as *V. vinifera*. Although development time was short and the survivorship high on *T. officinale*, it did not offer a suitable substrate for oviposition.

On most flowers or fruits preferred as oviposition sites, larval performance was also the best except for *P. cerasus*. The opposite was observed with *T. officinale*, on which very few eggs were laid although the larval performance was good. However, on flowers of *P. amygdaliformis*, *S. vulgaris*, *L. amplexicaule*, *C. recutita*, *M. pumila*, *N. oleander* and *Onopordum* sp. on which few eggs were laid the larval performance varied. On some of them the larvae developed well but, in others, larvae did not develop at all. Common weeds, such as *T. officinale*, *L. amplexicaule*, *C. recutita*, as well as the ornamentals, like *N. oleander* and *S. vulgaris*, could not be considered as alternate hosts. Peach and plum orchards adjacent to vineyards must be under consideration in control programmes as they may serve as potential hosts.

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