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Prior Experience Affects the Oviposition Behavior in Evania appendigaster (L.)(Hymenoptera: Evaniidae)【Research report】

蜚蠊瘦蜂先前產卵經驗影響其產卵行為【研究報告】

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Abstract

We evaluated the effect of prior ovipositional experience on the oviposition of Evania appendigaster (L.) (Hymenoptera: Evaniidae). Prior experience reduced the total time of the oviposition sequence; the preoviposition quiescent stage occupied most of the time for oviposition and was the most important plastic behavioral stage. If oviposition experience was withheld for more than three days, females seemed to forget what they had learned and acted as naive females. Booster experience did not decrease total time to finish the sequence of oviposition behavior.

摘要

本文評估蜚蠊瘦蜂(Evania appendigaster (L.))先前產卵經驗對其產卵行為之效應。先前經驗減少蜚蠊瘦蜂系列產卵行為之時間，產卵前靜止期佔系列產卵行為最多之時間，且亦是最重要的可塑期。如先前產卵經驗超過三天，雌瘦蜂忘記先前所學，好似未曾有產卵經驗的雌蟲一樣。重覆先前產卵經驗並不能減少全部系列產卵行為之時間。

Key words: Evania appendigaster, Periplaneta americana, behavior, learning.

關鍵詞: 瘦蜂、美洲蜚蠊、行為、學習

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Prior Experience Affects the Oviposition Behavior in *Evania appendigaster* (L.) (Hymenoptera: Evaniidae)

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ABSTRACT

We evaluated the effect of prior ovipositional experience on the oviposition of *Evania appendigaster* (L.) (Hymenoptera: Evaniidae). Prior experience reduced the total time of the oviposition sequence; the preoviposition quiescent stage occupied most of the time for oviposition and was the most important plastic behavioral stage. If oviposition experience was withheld for more than three days, females seemed to forget what they had learned and acted as naive females. Booster experience did not decrease total time to finish the sequence of oviposition behavior.

Key words: *Evania appendigaster*, *Periplaneta americana*, behavior, learning.

Introduction

In four species of aphidiid wasps, prior oviposition experience was found to affect host selection (Chow and Mackauer, 1992). Oviposition experience also reduced the approach time of *Ooencyrtus kuvanae*; the more experience in oviposition the wasp had acquired the less oviposition time needed (Lee and Lee, 1989; Lee *et al*., 1989). Females with oviposition experience on a host pupa are more likely than naive females to walk upwind in kairomone-laden air and to do so more rapidly (Carde and Lee, 1989). Females of the polyphagous ichneumonid parasitoid *Exeristes roborator* demonstrate associative learning by responding with ovipositor probes into the habitat alone (Wardle and Borden, 1985; 1991).

The ensign wasp *Evania appendigaster* is a solitary parasitoid of cockroach. It can be found in temperate and subtropical areas (Townes, 1949). Its hosts include *Periplaneta americana*, *P. australasiae*, *P. brunea*, *Blatta orientalis*, *Cutilia soror*, and *Neostylopyga rhombifolia* (Lebeck, 1991). Its developmental period lasts for about 38-40 days, and the longevity of adults is about 13 to 15 days in the laboratory (Yeh and Mu, 1994a). *E. appendigaster* shows a fixed action pattern of oviposition behavior on the ootheca of *P. americana*. Its oviposition sequence can be divided into seven steps: (1) host contact (with antennal drumming), (2) ovipositor extension and

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tapping, (3) preoviposition quiescence, (4) drilling, (5) ovipositing, (6) withdrawal, and (7) departure.

Females are attracted to host ootheca. They contact the ootheca by antennal drumming, then either fly away or stay on it. The wasps extend the ovipositor and tap the ootheca surface. It takes about 10 minutes for the wasps to locate the "right spot", and complete the preoviposition quiescent stage. Females move their abdomen up and down, drill the ovipositor into the ootheca, pull it out, and drill repeatedly, looking for a good position. They then just sit on ootheca and lay eggs followed by withdrawal of the ovipositor and departure. The effects of prior oviposition experience on the oviposition behavior of the ensign wasp were tested in the laboratory. In this paper, we define oviposition as actual egg laying by females, oviposition behavior as all seven behavioral steps, and an oviposition event as a single sequence of oviposition behavior.

Materials and Methods

Rearing of *P. americana* and *E. appendigaster* was performed using the methods of Yeh and Mu (1994a, b). Oothecae used in the experiments were deposited by American cockroaches within 24 h of the experiments. A single naive female (i.e., without previous oviposition experience) ensign wasp (three days old and mated at the day after emergence) was released in a lid-covered plastic cup (9 cm dia. X 5 cm) containing one ootheca, and the wasp oviposition behavior was observed. Detailed oviposition behavior and total oviposition times were recorded with a V8 video camera.

The following experiments were conducted: (1) 1st experiment: consecutive ovipositions of three eggs on three oothecae on the 1st day (indicated as 1-1-1); (2) 2nd experiment: oviposition of three eggs, one each on 1st, 2nd, and 3rd days, respectively (1-2-3); (3) 3rd experiment: oviposition of three eggs, one each on the 1st, 2nd, and 5th days, respectively (1-2-5); (4) 4th experiment: oviposition of three eggs, one each on the 1st, 2nd, and 7th days, respectively (1-2-7); (5) 5th experiment: oviposition of three eggs, one each on the 1st, 2nd, and 9th days, respectively (1-2-9); (6) 6th experiment: oviposition of 2 eggs, one each on the 1st, and 4th days, respectively (1-4); (7) 7th experiment: oviposition of three eggs, one on the 1st day and two consecutive ovipositions on the 5th day (1-5-5); (8) 8th experiment: oviposition of one egg on the 1st day and two consecutive ovipositions on the 6th day (1-6-6); (9) 9th experiment: oviposition of one egg on the 1st day, and two consecutive ovipositions on the 8th day (1-8-8).

Wasps were exposed to consecutive oviposition experiences to determine if prior experience reduces the time of oviposition. Wasps with prior oviposition experience were held without additional experience for one day (1-2-3), three days (1-2-5) (1-4), five days (1-2-7), or seven days (1-2-9), or in other experiments, for four days (1-5-5), five days (1-6-6), or seven days (1-8-8) followed by consecutive ovipositions, to determine how long experience could be withheld, and if booster experience could increase the oviposition efficiency and shorten the time of the oviposition sequence. Each experiment was done with eight replications. All experiments were carried out in a walk-in growth chamber (180 X 180 X 180 cm) at 26-28℃, 70-90% RH, with a L:D = 12:12 photoperiod.

For data analysis, we used the split-plot design. In the main plot, ovipsoitional event treated as the treatment of one factor and the female as a block, arranged in a randomized complete block design. The oviposional stages were treated as treatments of the second factor, and were assigned to subplots within each main plot. Significance between treatments was evaluated and followed by range test (SAS, 1988). All values are presented as mean ±

SD.

Results

Wasps were exposed to consecutive oviposition experiences on the same day (1-1-1) to determine if prior experience reduced the time of oviposition (Table 1). The total time needed to finish the sequence of behavior was significantly shorter for experienced than for naive wasps. Time spent in the preoviposition quiescent stage and the withdrawal stage was significantly shorter in experienced wasps than in naive wasps. The total time spent by experienced wasps to finish the sequence of behavior was not significantly different between oviposition events II and III (OEII & OEIII). There were significant differences in oviposition behavioral stages between experienced and naive wasps. The stage of quiescent was significantly longer than the other stage both in the experienced wasps and the naive wasps. The stage of oviposition was the next longer stage in both experienced and naive wasps.

If booster experiences took place within three days, the total time to finish the sequence of oviposition behavior was significantly shorter in experienced wasps (OEII) (i.e., 1-1, 1-2, 1-4) (Tables 1, 2, 4, 5, and 6) than in naive wasps. In addition, the preoviposition quiescent stage was significantly shorter in experienced than in naive wasps. But, when oviposition experience was withheld for more than three days (i.e., 1-5, 1-6, 1-8) (Tables 7, 8, and 9), the total time to finish the sequence of oviposition behaviors were not significantly different between experienced and

Table 1. Mean ovipositional time (sec.) ± SD of 3 consecutive ovipositions within 1 day (1-1-1) in *E. appendigaster*

Oviposition Behavior	Mean ovipositional time (sec.) ± SD (n = 8)		
	OE I [1]	OE II	OE III
1. Host contact	16.6 ± 5.6a [2]	19.4 ± 8.5a	6.3 ± 7.8a
2. Tapping	93.6 ± 66.7a	42.5 ± 13.5a	70.1 ± 35.1a
3. Quiescence	560.5 ± 188.6a	342.6 ± 166.7b	375.4 ± 156.6b
4. Drilling	95.9 ± 86.9a	39.1 ± 27.8a	101.3 ± 63.9a
5. Oviposition	173.3 ± 40.3a	172.9 ± 69.7a	142.0 ± 20.7a
6. Withdrawal	71.5 ± 12.4a	55.6 ± 8.3a	46.6 ± 10.4a
Total	1011.4 ± 299.2a	672.1 ± 168.3b	751.7 ± 169.3b

1.) OE = ovipositional event (I, II, III).

2.) Means in the same row followed by the same letter are not significantly different by Fisher's LSD test ($p < 0.05$).

Table 2. Mean ovipositional time (sec.) ± SD of 3 ovipositions with 1-day intervals (1-2-3) in *E. appendigaster*

Oviposition behavior	Mean ovipositional time (sec.) ± SD (n = 8)		
	OE I (1st d) [1]	OE II (2nd d)	OE III (3rd d)
1. Host contact	28.5 ± 8.8a [2]	16.0 ± 7.9b	19.0 ± 10.6b
2. Tapping	141.8 ± 92.1a	76.3 ± 59.6b	57.3 ± 29.2b
3. Quiescence	618.1 ± 258.8a	411.9 ± 190.1b	359.8 ± 162.1b
4. Drilling	68.8 ± 49.2a	25.0 ± 8.0a	36.9 ± 27.5a
5. Oviposition	193.8 ± 106.1a	157.0 ± 42.5a	144.0 ± 44.2a
6. Withdrawal	63.2 ± 19.8a	49.1 ± 14.9a	52.8 ± 12.5a
Total	1114.2 ± 290.8a	735.3 ± 175.6b	669.8 ± 202.6b

1.) OE = ovipositional event (I, II, III).

2.) Means in the same row followed by the same letter are not significantly different by Fisher's LSD test ($p < 0.05$).

Table 3. Mean ovipositional time (sec.) ± SD of 3 ovipositions with 1-day and 3-day intervals (1-2-5) in *E. appendigaster*

Oviposition behavior	Mean ovipositional time (sec.) ± SD (n = 8)		
	OE I (1st d) [1]	OE II (2nd d)	OE III (3rd d)
1. Host contact	29.1 ± 24.1a [2]	19.3 ± 14.1a	15.4 ± 4.4a
2. Tapping	129.9 ± 124.2a	32.3 ± 11.4a	76.3 ± 44.7a
3. Quiescence	667.7 ± 262a	481.9 ± 121b	449.3 ± 129.9b
4. Drilling	101.1 ± 75a	38.1 ± 27.2a	49.3 ± 34.7a
5. Oviposition	165.4 ± 16.4a	140.1 ± 36.9a	170.7 ± 55.4a
6. Withdrawal	58.9 ± 14a	51.3 ± 10.2a	55.9 ± 6.3a
Total	1152.1 ± 259.9a	763 ± 244.4b	816.9 ± 282.1b

1.) OE = ovipositional event (I, II, III).

2.) Means in the same row followed by the same letter are not significantly different by Fisher's LSD test ($p < 0.05$).

Table 4. Mean ovipositional time (sec.) ± SD of 3 ovipositions with 1-day and 5-day intervals (1-2-7) in *E. appendigaster*

Oviposition behavior	Mean ovipositional time (sec.) ± SD (n = 8)		
	OE I (1st d) [1]	OE II (2nd d)	OE III (3rd d)
1. Host contact	20.8 ± 6.1a [2]	14.6 ± 3.3a	16 ± 4.6a
2. Tapping	172.3 ± 90.8a	63.3 ± 39.5b	76.8 ± 34.8b
3. Quiescence	562.3 ± 143.4a	385.8 ± 102.3b	589.3 ± 102.2a
4. Drilling	47.3 ± 37.8a	22.1 ± 8a	37.1 ± 21.3a
5. Oviposition	161.9 ± 83.3a	134.4 ± 23.4a	197.4 ± 95.5a
6. Withdrawal	56.3 ± 9.7a	45.8 ± 6.9a	60 ± 11.6a
Total	1020.9 ± 138.4a	666 ± 146.1b	976.6 ± 169.2a

1.) OE = ovipositional event (I, II, III).

2.) Means in the same row followed by the same letter are not significantly different by Fisher's LSD test ($p < 0.05$).

Table 5. Mean ovipositional time (sec.) ± SD of 3 ovipositions with 1-day and 7-day intervals (1-2-9) in *E. appendigaster*

Oviposition behavior	Mean ovipositional time (sec.) ± SD (n = 8)		
	OE I (1st d) [1]	OE II (2nd d)	OE III (3rd d)
1. Host contact	45.6 ± 21.2a [2]	33.6 ± 22.1a	24.9 ± 18a
2. Tapping	77 ± 48.9a	85.3 ± 71.9a	58 ± 36.3a
3. Quiescence	822 ± 298.4a	385.6 ± 105.3b	731.9 ± 205.3a
4. Drilling	68.3 ± 29.1a	37 ± 13.1a	86.4 ± 74.1a
5. Oviposition	183.7 ± 61.1a	143.1 ± 42.1a	165.6 ± 53.9a
6. Withdrawal	58.6 ± 16.6a	59 ± 11.8a	72 ± 11.1a
Total	1255.2 ± 380.7a	743.6 ± 164.7b	1138.8 ± 176.4a

1) OE = ovipositional event (I, II, III).

2) Means in the same row followed by the same letter are not significantly different by Fisher's LSD test ($p < 0.05$).

naive wasps, and the quiescent period was not significantly shorter either.

For same day (1-1-1) (Table 1), consecutive day (1-2-3) (Table 2) and consecutive day followed by three-day break (1-2-5) (Table 3) experiments, the total times to finish the sequence of oviposition behavior of experienced wasps in OEIII and in OEII were not

Table 6. Mean ovipositional time (sec.) ± SD of 2 ovipositions with 3-day interval (1-4) in *E. appendigaster*

Oviposition behavior	Mean ovipositional time (sec.) ± SD (n = 8)	
	OE I (1st d) [1]	OE II (2nd d)
1. Host contact	19.8 ± 8.5a [2]	18.8 ± 12.3a
2. Tapping	77 ± 37.3a	85.3 ± 46.8a
3. Quiescence	692.9 ± 213.7a	428.5 ± 245.6b
4. Drilling	93 ± 91.9a	30 ± 15.1a
5. Oviposition	157.4 ± 44.1a	230.3 ± 174.2a
6. Withdrawal	59 ± 11.2a	51.5 ± 10.2a
Total	1099.1 ± 225.8a	844.4 ± 234b

1) OE = ovipositional event (I, II).
2) Means in the same row followed by the same letter are not significantly different by Fisher's LSD test ($p < 0.05$).

Table 7. Mean ovipositional time (sec.) ± SD of 3 ovipositions with 4-day interval followed by consecutive ovipositions (1-5-5) in *E. appendigaster*

Oviposition behavior	Mean ovipositional time (sec.) ± SD (n = 8)		
	OE I (1st d) [1]	OE II (2nd d)	OE III (3rd d)
1. Host contact	21.9 ± 6.8a [2]	16.9 ± 4.8a	16.8 ± 3.5a
2. Tapping	101.9 ± 52.8a	66.1 ± 14.4a	59.0 ± 32.6a
3. Quiescence	592.8 ± 149.6a	558.6 ± 122.9a	409.6 ± 102.9b
4. Drilling	84.6 ± 76.8a	54.1 ± 33.7a	66.5 ± 32.4a
5. Oviposition	183.4 ± 74.4a	178.5 ± 42.4a	147.6 ± 32.9a
6. Withdrawal	64.3 ± 13.9a	60.9 ± 9.5a	55.9 ± 6.9a
Total	1048.9 ± 165.9a	935.1 ± 119.6a	755.4 ± 119.4b

1) OE = ovipositional event (I, II, III).
2) Means in the same row followed by the same letter are not significantly different by Fisher's LSD test ($p < 0.05$).

significantly different. Booster experience for more than three days (1-2-7, 1-2-9) (Tables 4 and 5), resulted in significantly longer total times to finish the sequence of OEIII than of OEII. The preoviposition quiescent stage of wasps in OEII was significantly shorter than in OEI. There were no significant differences in total time between OEIII and OEI. Booster experiences on the same day, after four, five, or seven days (1-5-5, 1-6-6, and 1-8-8) (Tables 7, 8, and 9) resulted in significantly shorter total times for OEIII than for OEII. The preoviposition quiescent stage of wasps for OEIII was significantly shorter than that for OEII.

Discussion

The total times needed to complete the oviposition sequence were consistent in naive ensign wasp females. Naive wasps followed the seven-step oviposition behavior patterns, and times spent in preoviposition quiescent stage were similar to those reported in the study by Yeh and Mu (1994b). The experienced ensign wasp females also followed the same pattern of oviposition behavior.

The postoviposition departure stage was not mentioned in this study because the wasps continuously stayed in the cage for another oviposition. Time to finish the sequence of oviposition behavior is influenced by the age of the oothecae (Yeh and Mu, 1994b). In order to diminish variation,

Table 8. Mean ovipositional time (sec.) ± SD of 3 ovipositions with 5-day interval followed by consecutive ovipositions (1-6-6) in *E. appendigaster*

Oviposition behavior	Mean ovipositional time (sec.) ± SD (n = 8)		
	OE I (1st d) [1]	OE II (2nd d)	OE III (3rd d)
1. Host contact	18.3 ± 9a [2]	16.9 ± 4.2a	14.9 ± 5a
2. Tapping	85.4 ± 70a	75.8 ± 46.1a	73.4 ± 33a
3. Quiescence	643.9 ± 266.4a	586.4 ± 89.7a	393.5 ± 104.8b
4. Drilling	33.4 ± 20.3a	45.4 ± 39a	28.3 ± 9.3a
5. Oviposition	144.9 ± 29.5a	168.8 ± 67a	131.2 ± 27.3a
6. Withdrawal	58.8 ± 18.2a	52.9 ± 141.6a	53.0 ± 11.1a
Total	984.7 ± 209.2a	946.2 ± 141.6a	694.3 ± 140.2b

1) OE = ovipositional event (I, II, III).

2) Means in the same row followed by the same letter are not significantly different by Fisher's LSD test ($p < 0.05$).

Table 9. Mean ovipositional time (sec.) ± SD of 3 ovipositions with 7-day interval followed by consecutive ovipositions (1-8-8) in *E. appendigaster*

Oviposition behavior	Mean ovipositional time (sec.) ± SD (n = 8)		
	OE I (1st d) [1]	OE II (2nd d)	OE III (3rd d)
1. Host contact	23.9 ± 16.1a [2]	27.5 ± 22a	22.3 ± 7.2a
2. Tapping	93.6 ± 66.7a	42.3 ± 13.5a	70.1 ± 35.1a
3. Quiescence	562.5 ± 213.8a	446.6 ± 156.3a	293.8 ± 86.4b
4. Drilling	69.9 ± 54a	58.9 ± 44.4a	42.9 ± 33.6a
5. Oviposition	164.8 ± 43.6a	198.4 ± 179.3a	130.6 ± 24.4a
6. Withdrawal	63.4 ± 2.7a	66.3 ± 12.7a	54.5 ± 19.7a
Total	978.1 ± 285.8a	840 ± 188.9a	614.2 ± 115.3b

1) OE = ovipositional event (I, II, III).

2) Means in the same row followed by the same letter are not significantly different by Fisher's LSD test ($p < 0.05$).

three-day-old ensign wasps and 24-h-old oothecae were used.

Little evidence of learning was found in our study, but the observed result of ovipositing experience is consistent with some definition of learning, e.g., learning as a "change in behavior with experience" (Papaj and Prokopy, 1989). Experienced females learn to recognize the right oothecae of host and egg-laying site.

Parasitoid's searching behavior can be affected by experience. These experiences involve contacts with specific host-derived stimuli that the wasps recognize innately. The wasps may also learn by associate learning, e.g., to " learn to respond to unrecognized stimuli by linking these new stimuli to the contact stimuli" (Turling *et al*., 1993).

Arthur (1971) demonstrated learning of novel odors by the ichneumoid *Nemeritis canescens.* Vinson *et al.* (1966), and Wardle and Borden (1988) found similar associations. The physiological processes behind associative learning have not yet been explained. Associative learning is not limited to olfactory stimuli, as parasitoids are also able to link visual and mechanosensory stimuli (Turling *et al.*, 1993). Further studies are needed to identify the exact stimuli link to the associative learning in *E. appendigaster.*

Prior experience can reduce the time to finish the sequence of a second oviposition on the same day, and experience can be withheld up to three days. After three days, the female will forget what has been learned and act as a naive female.

These ovipostion behaviors are similar to that of *Ooencyrtus kuvanae*, the egg parasitoid of *Lymantria dispar* (Lee and Lee, 1989).

Booster experience did not further decrease the total time to finish the sequence of oviposition behavior. After three days, females will forget the experience. In a previous study, lack of continued experience for more than four days resulted in the insect forgetting what had been learned (Papaj and Prokopy, 1989) and a return to the naive state.

In general, preoviposition quiescence occupied most of the time spent in oviposition. In some experiments, the preoviposition host contact, tapping, and post-oviposition withdrawal stages of experienced wasps were shorter than in naive females. The preoviposition quiescent stage is the stage where the ensign wasp females locate the position of the ootheca using the ovipositor, and it remains quiescent for most of the time. Yeh and Mu (1994b) postulated that females secrete chitin- or protein-denaturing enzymes to dissolve the shell of the ootheca, which is thought to accelerate the penetration of the ovipositor. Experienced females probably need less time to locate the right spot for penetration by the ovipositor than do naive females. That is why the preoviposition quiescent stage of experienced females was shorter than that of naive females in this study.

The preoviposition host contact stage was shorter in the experienced female in three ovipositions with one day intervals (Table 2). In the host contact stage, the female drumson the ootheca with its antennae consistently (Yeh and Mu, 1994a). Antennae drumming is probably for host identification. Experienced females need less time for host identification. The host contact stage was also shorter in the experienced female in ovipostional event II (OEII). But after five days, the host contact stage of ovipositional event II (OEII) and ovipositional event III (OEIII) were not significantly different (Table 4). The host contact stages of ovipositional event I (OEI) and ovipositional event II (OEII) were not significantly different either (Table 7). After five days, females forgot what have learned and acted as inexperience females.

The tapping stage of the experienced female in ovipositional event III (OEIII) was shorter in three ovipositions with one day interval (Table 2). But the tapping stages of ovipositional event I (OEI) and ovipositional event II (OEII), and ovipositional event II (OEII) and ovipositional event III (OEIII) were not significantly different (Table 2). In the tapping stage, female extended ovipositor and tapping the ootheca for location identification (Yeh and Mu, 1994a). Experienced females need less times for location identification. The tapping stage of experienced females was also shorter than that of naive females in OEII (Table 4). But after five days, the tapping stages of ovipsitional event II (OEII) and ovipositional event III (OEIII) were not significantly different. The tapping stages of ovipositional event I (OEI) and ovipositional event II (OEII) were not significantly different either (Table VII). After five days, females forgot what they had learned and acted as inexperience females.

The longevity of *E. appendigaster* adults in the laboratory has been reported to be 13.3 days for females and 14.9 days for males (Yeh and Mu, 1994a). By offering 10% table sugar solution, both males and females could survive for more than 30 days. Even 12-day-old wasps in the 9th experiment were not treated as old wasps under the laboratory rearing conditions.

The experienced ensign wasp probed using her ovipositor, but some (ca.10%) could not penetrate the ootheca, or the ovipositor was not ready for probing due to morphological damage to the ovipositor and the stylets. Such wasps tried to drill but failed to penetrate the oothecae and left, terminating the oviposition behavior. Those that terminated the oviposition behaviors were not counted in this study.

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蜚蠊瘦蜂先前產卵經驗影響其產卵行為

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摘　要

本文評估蜚蠊瘦蜂(*Evania appendigaster* (L.))**先前產卵經驗對其產卵行為之效應。先前經驗減少蜚蠊瘦蜂系列產卵行為之時間，產卵前靜止期佔系列產卵行為最多之時間，且亦是最重要的可塑期。如先前產卵經驗超過三天，雌瘦蜂忘記先前所學，好似未曾有產卵經驗的雌蟲一樣。重覆先前產卵經驗並不能減少全部系列產卵行為之時間。**

關鍵詞：瘦蜂、美洲蜚蠊、行為、學習。