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## Effects of Male Interference on Oviposition Behaviour of the Adzuki Bean Weevil, *Callosobruchus chinensis* (L.), (Coleoptera: Bruchidae) 【Research report】

### 綠豆象(*Callosobruchus chinensis* (L.)) (Coleoptera: Bruchidae)雄蟲干擾對雌蟲產卵行為之影響【研究報告】

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\*通訊作者E-mail: [bean weevil](mailto:beanweevil@yabee.com.tw), male harassment, mean crowding, total eggs laid.

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#### Abstract

The females of *Callosobruchus chinensis* (L.) produce a nearly uniform distribution of eggs on beans. This behaviour result in minimizing larval competition within beans, and increasing survival rate of larva. Since female behaves reluctantly when mating has proceeded, the presence of virgin male would induce solicitation behaviour which causes harassment to female. Further, female spend most of time on oviposition and rest, the solicitation behaviour of male therefore introduces interference on oviposition behaviour of female. In this study, we manipulate differences in time schedule of offering virgin male and density of virgin males to test the effects of male interference on egg dispersion behaviour, total eggs laid and longevity of female. The total number of eggs laid by females paired with 4 virgin males were significantly lower than that of females paired with one virgin male for 9 hours. Therefore, high density of virgin male which introduced high frequency of interference resulted in decreasing fecundity of females. When offering virgin male with different time schedule, female which were paired with 2 virgin males on the 24 th hour from the beginning of the experiment showed significantly higher mean crowding on the 2 nd day than female paired with 2 virgin males at the beginning of the experiment, but were not different the day after. This result suggested that male solicitation behaviour caused interference on female egg dispersion behaviour but female showed adaptation immediately after one day. On the contrary to previous prediction, high density of males didn't result in increasing mean crowding of eggs. Female paired with one male for 9 hours showed higher mean crowding from the 2 nd day than female paired with males. The two level of effects by manipulation on time scheduling and density of virgin males suggested that the effect of male harassment on fitness of offspring were complex and need a further study. Comparison of trade-offs between longevity and total number of eggs laid by females suggested that females which were paired with more males would cause reduction in both longevity and total number of eggs laid. Therefore, excessive male solicitation behaviour would cause interference which would decrease fitness of female.

#### 摘要

綠豆象(*Callosobruchus chinensis* (L.))具均勻產卵的特性，可減少其幼蟲競爭，使子代適存值增大。然而當有雄蟲存在時，雄蟲的求偶行為，會對雌蟲產生一定程度的干擾，進而影響產卵分布，降低子代適存值。本研究中以不同供蟲時間及不同的雄蟲密度處理雌蟲，記錄雌蟲的產卵數、產卵分布、以及壽命。試驗結果發現雌蟲與4隻雄蟲配對，產卵數明顯低於與1隻雄蟲配對之雌蟲，顯示雄蟲密度過高時會降低雌蟲產卵數。當雌蟲突然遭受雄蟲求偶干擾時，卵平均擁擠度會顯著上升，但這種效應在處理後一天即消失。顯示雄蟲的突然干擾會造成產卵中雌蟲行為的改變，導致雌蟲產卵不均勻，但雌蟲能在短時間內即產生適應行為。以不同密度雄蟲與雌蟲配對時，單隻雌蟲產卵之平均擁擠度，高於多隻雄蟲處理組，因此反而無法由平均擁擠度看到干擾效應的存在。故雄蟲的干擾對子代競爭的影響，是正面或負面則尚無定論。若從雌蟲生殖花費(cost of reproduction)權衡(trade-off)的角度來探討雄蟲的干擾效應，可知單隻雌蟲之壽命與總產卵數皆顯著高於4隻雄蟲處理組。顯示過多的雄蟲干擾會降低雌蟲壽命與生殖力，進而降低雌蟲適存值。

**Key words:** bean weevil, male harassment, mean crowding, total eggs laid.

**關鍵詞:** 豆象、求偶干擾、平均擁擠度、產卵數

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# 綠豆象(*Callosobruchus chinensis* (L.)) (Coleoptera: Bruchidae) 雄蟲干擾對雌蟲產卵行爲之影響

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## 摘 要

綠豆象(*Callosobruchus chinensis* (L.))具均勻產卵的特性，可減少其幼蟲競爭，使子代適存值增大。然而當有雄蟲存在時，雄蟲的求偶行爲，會對雌蟲產生一定程度的干擾，進而影響產卵分布，降低子代適存值。本研究中以不同供蟲時間及不同的雄蟲密度處理雌蟲，記錄雌蟲的產卵數、產卵分布、以及壽命。試驗結果發現雌蟲與4隻雄蟲配對，產卵數明顯低於與1隻雄蟲配對之雌蟲，顯示雄蟲密度過高時會降低雌蟲產卵數。當雌蟲突然遭受雄蟲求偶干擾時，卵平均擁擠度會顯著上升，但這種效應在處理後一天即消失。顯示雄蟲的突然干擾會造成產卵中雌蟲行爲的改變，導致雌蟲產卵不均勻，但雌蟲能在短時間內即產生適應行爲。以不同密度雄蟲與雌蟲配對時，單隻雌蟲產卵之平均擁擠度，高於多隻雄蟲處理組，因此反而無法由平均擁擠度看到干擾效應的存在。故雄蟲的干擾對子代競爭的影響，是正面或負面則尚無定論。若從雌蟲生殖花費(cost of reproduction)權衡(trade-off)的角度來探討雄蟲的干擾效應，可知單隻雌蟲之壽命與總產卵數皆顯著高於4隻雄蟲處理組。顯示過多的雄蟲干擾會降低雌蟲壽命與生殖力，進而降低雌蟲適存值。

**關鍵詞：**豆象、求偶干擾、平均擁擠度、產卵數。

## 前 言

綠豆象(*Callosobruchus chinensis* (L.)), adzuki bean weevil)屬鞘翅目豆象科(Bruchidae)。在實驗室28°C恆溫飼養下，羽化後2小時之雌、雄蟲即可進行交尾(Lan, unpublished)。交尾後雌蟲即可進行產卵。雌蟲產卵於寄主豆表面，幼蟲在孵化後鑽入豆中取食，成蟲羽化後在寄主豆表皮咬破一圓形孔而離開寄主豆。由於整個幼蟲期與蛹期

都在寄主豆中完成，因此雌蟲選擇的寄主豆攸關子代的適存值。在多種豆象的研究中已證實雌蟲具有均勻產卵的特性，以避免子代在同一顆寄主豆上競爭資源，導致子代適存值降低(Mitchell, 1975)。

豆象雌蟲交尾後大部分時間均花費在產卵上，此時若有雄蟲進行求偶，雌蟲多半會拒絕接受(Wasserman, 1985)。這是由於在多次交尾的利益上，兩性是不平衡的。一般而言，雄蟲可透過多次交尾而獲得大量的子

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代，而雌蟲透過多次交尾所增加的子代數則有限(Fox, 1993; Fox, *et al.*, 1995)。因此在交尾的利益上，兩性存在著性別衝突(sexual conflict) (Krebs and Davies, 1993)。根據四紋豆象(*Callosobruchus maculatus* (Fab.))研究指出，雌蟲在產卵時易遭受雄蟲的求偶干擾而中斷其產卵行為(Wasserman, 1985)。然而，雄蟲的求偶行為對雌蟲及其子代的影響研究則付之闕如。綠豆象亦具有均勻產卵的特性(Lan, unpublished)，雌蟲產卵分布均勻與否關係著子代之適存值。本試驗目的在探討綠豆象雌蟲在產卵時，雄蟲求偶行為對雌蟲產卵行為，包括產卵分布、產卵數及壽命的影響，以期瞭解雄蟲求偶行為對雌蟲適存值之作用，即雌蟲對干擾行為之適應。試驗首先以不同供蟲時間處理，探討雄蟲干擾對雌蟲產卵分布的影響是否存在？其次比較不同雄蟲密度處理對雌蟲產卵分布之影響；最後則探討不同處理組雌蟲產卵數及壽命受雄蟲干擾之效應。

## 材料與方法

試驗用之綠豆象品系係於民國八十三年於嘉義朴子之倉儲綠豆中取得蟲源，在室內於28°C之全暗生長箱中，以省產粉質綠豆(*Vigna radiata*)飼養，室內飼養代數逾90代。

為探討雄蟲求偶行為是否對雌蟲的產卵行為產生干擾進而影響其產卵分布，本試驗以不同的雄蟲密度為處理條件，以瞭解在多隻雄蟲處理下，雌蟲遭受到較高頻率的求偶干擾下，其產卵行為的改變。試驗中亦同時以不同的供蟲時間，觀察雄蟲求偶行為對產卵中雌蟲的作用。本試驗以羽化12小時內之未交尾雌、雄蟲，置入內含50顆綠豆之直徑5.5 cm 玻璃培養皿中作配對，試驗設計如

下：(A)雌、雄蟲各一隻，配對9小時後將雄蟲挑除，雌蟲自配對9小時開始後即不再受雄蟲求偶干擾，此處理為對照組；(B)雌、雄蟲各一隻，配對後第9小時將雄蟲挑除，第24小時再提供2隻未交尾雄蟲，以測試雄蟲突然干擾的作用；(C)一隻雌蟲與二隻雄蟲配對。(D)一隻雌蟲與四隻雄蟲配對。各處理組均為20重複。記錄各處理組雌蟲每日產卵數、產卵分布及壽命。在研究產卵分布時，我們採用卵平均擁擠度(Mean crowding,  $m^*$ )為指標(Lloyd, 1967)，此數值是計算平均在每顆豆上與每粒卵共存的卵數。當平均擁擠度高時代表產卵分布趨於不均勻，反之則產卵趨於均勻。

不同供蟲時間之(B)與(C)處理中，雌蟲每日產卵分布，分別以t-test進行比較，以確定雄蟲干擾效應是否存在及持續時間；不同雄蟲密度處理組(A)、(C)及(D)之雌蟲每日產卵分布，則進行變方分析，並以費雪最小顯著差異試驗法(Fisher's PLSD)進行處理效應之比較。另外，亦比較各處理組雌蟲之每日累積產卵數、總產卵數及壽命，以瞭解雄蟲干擾之處理效應。

## 結 果

在不同的雄蟲密度處理下，三組的每日累積產卵數在試驗第4天之後即有顯著差異(表一)。當雄蟲數過多，與雌蟲比例達1:4時，會產生干擾作用而不利於雌蟲產卵。在4隻雄蟲處理組(處理組D)，雌蟲自第4天起累積產卵數即顯著少於無雄蟲組(處理組A)，顯示在多隻雄蟲干擾下，會使雌蟲的產卵數降低。

以不同供蟲時間處理綠豆象雌蟲，在試驗第24小時提供2隻雄蟲時(處理組B)，卵平均擁擠度明顯上升，且大於在試驗開始時

表一 不同雄蟲密度和供蟲時間處理之綠豆象雌蟲累積產卵數之比較

Table 1. Number of daily accumulated eggs laid by females of *C. chinensis* treated with different numbers of males

Day\Treatment**	Accumulated eggs laid (mean ± se)*			F (p value)
	1 female (A)	1 female + 2 males (C)	1 female + 4 males (D)	
1	21.0 ± 1.6 a	22.1 ± 2.0 a	25.6 ± 1.9 a	1.66 (p = 0.2001)
2	40.2 ± 1.9 a	38.9 ± 1.9 a	41.4 ± 2.5 a	0.33 (p = 0.7235)
3	52.2 ± 2.2 a	50.2 ± 1.9 a	47.4 ± 2.3 a	1.27 (p = 0.2891)
4	58.4 ± 2.9 a	53.9 ± 2.1 ab	49.4 ± 2.4 b	3.27 (p = 0.0455)
5	59.8 ± 3.0 a	55.4 ± 2.1 ab	50.7 ± 2.5 b	3.15 (p = 0.0506)
6	60.2 ± 3.0 a	56.4 ± 2.1 ab	51.1 ± 2.5 b	3.14 (p = 0.0512)
7	60.4 ± 2.9 a	56.5 ± 2.1 ab	51.4 ± 2.5 b	3.11 (p = 0.0523)
8	60.4 ± 2.9 a	56.5 ± 2.1 ab	51.4 ± 2.5 b	3.15 (p = 0.0508)

\* Means in the same row followed by the same letter are not significantly different by ANOVA ( $p > 0.05$ ).

\*\* 1) Female in treatment (A) was paired with one male at the beginning of the experiment; the male was discarded at the 9<sup>th</sup> hour.

2) Female in treatment (C) was paired with two males at the beginning of the experiment.

3) Female in treatment (D) was paired with four males at the beginning of the experiment.

即以2隻雄蟲處理之雌蟲(處理組C)(圖一), 顯示雄蟲在第24小時突然出現的求偶行為會對產卵中的雌蟲產生干擾, 致使其產卵分布較為不均勻。但此效應在試驗第三天即不存在, 顯示在此雄蟲密度下, 雌蟲在一段時間後即對雄蟲的求偶行為產生了適應性。

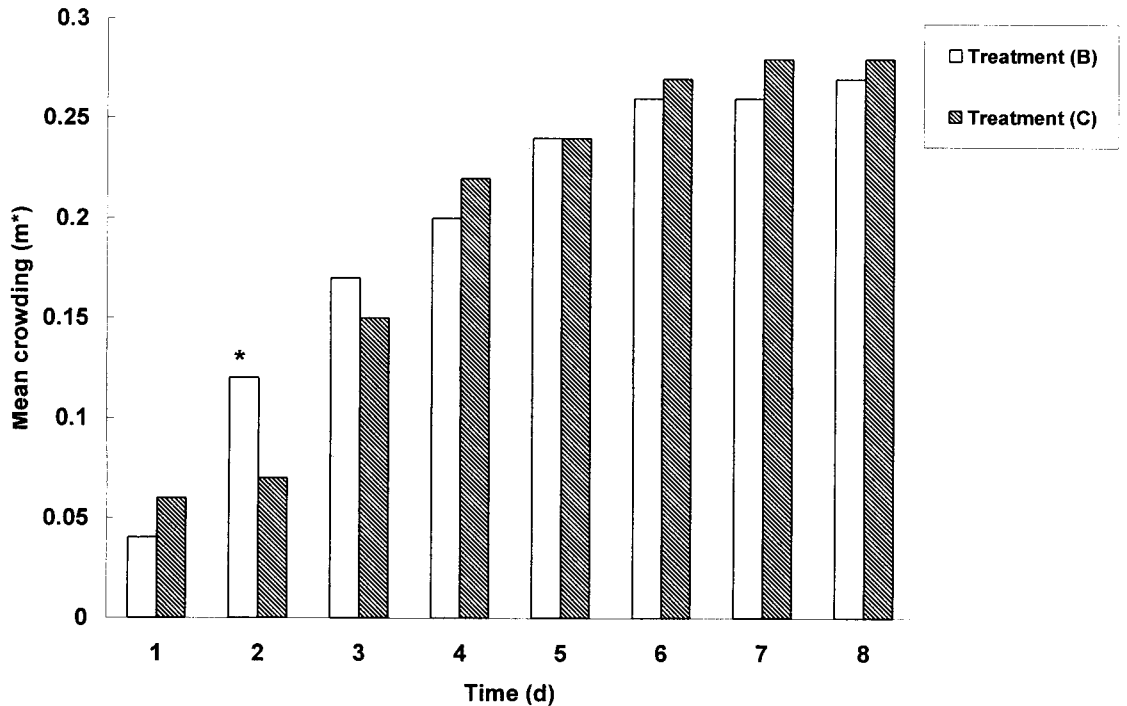
以不同的雄蟲密度處理綠豆象雌蟲, 無雄蟲處理組(處理A)之卵平均擁擠度在試驗第二天即與4隻雄蟲處理組(處理D)有顯著差異(圖二), 且在試驗第三天時亦與2隻雄蟲處理組(處理C)有顯著差異( $p = 0.0012$ ), 顯示在有雄蟲持續存在干擾時, 雌蟲的產卵行為反較趨向於均勻分布。

雄蟲的求偶干擾為雌蟲在壽命與產卵數間權衡上的限制因子。由圖三可知, 2隻雄蟲處理組(處理C)雌蟲雖與無雄蟲處理組(處理A)雌蟲之總產卵數無差異, 但壽命卻明顯地較短; 而處理A與B、B與C、D之雌蟲壽命雖無統計上之顯著差異, 但在處理A與D間雌蟲壽命則有顯著差異; 即在4隻雄蟲處理組(處理D), 雌蟲不僅在總產卵數少於無雄蟲處理組(處理A), 壽命亦較低, 顯示雄蟲求

偶干擾的另一項作用是造成雌蟲的壽命減少。

## 討 論

根據本試驗結果, 雄蟲的求偶干擾對雌蟲的產卵數、產卵分布、以及壽命均有影響。根據四紋豆象的研究結果, 雌蟲在接受多次交尾後, 每日產卵數會提高; 且在成蟲不取食的情況下, 雌蟲接受多次交尾可提高其壽命(Fox, 1993)。本試驗結果顯示, 當綠豆象雄蟲密度過高時, 雌蟲產卵數及壽命皆顯著降低; 在產卵數方面, 4隻雄蟲處理組(處理組D)雌蟲之產卵數顯著低於無雄蟲組(處理組A)(表一)。其原因可能為, 當雄蟲密度高時, 雄蟲不斷地求偶, 瓜分了雌蟲產卵的時間, 並且耗費過多的能量在拒絕交尾, 致使雌蟲的產卵數降低, 甚至壽命亦減少(圖三)。在本試驗處理中, 有處理A、C與D的雄蟲是一直與雌蟲存在的, 因此雄蟲的存在, 不但牽涉到致使雌蟲發生多次交尾的機率增加, 亦同時牽涉到增加雌蟲拒絕雄蟲



圖一 雄蟲供蟲時間對綠豆象雌蟲產卵擁擠度之影響。處理組 B：雌蟲與 1 隻雄蟲配對 9 小時後，雄蟲被挑除；在第 24 小時再提供 2 隻雄蟲。處理組 C：雌蟲在試驗開始時即與 2 隻雄蟲配對。

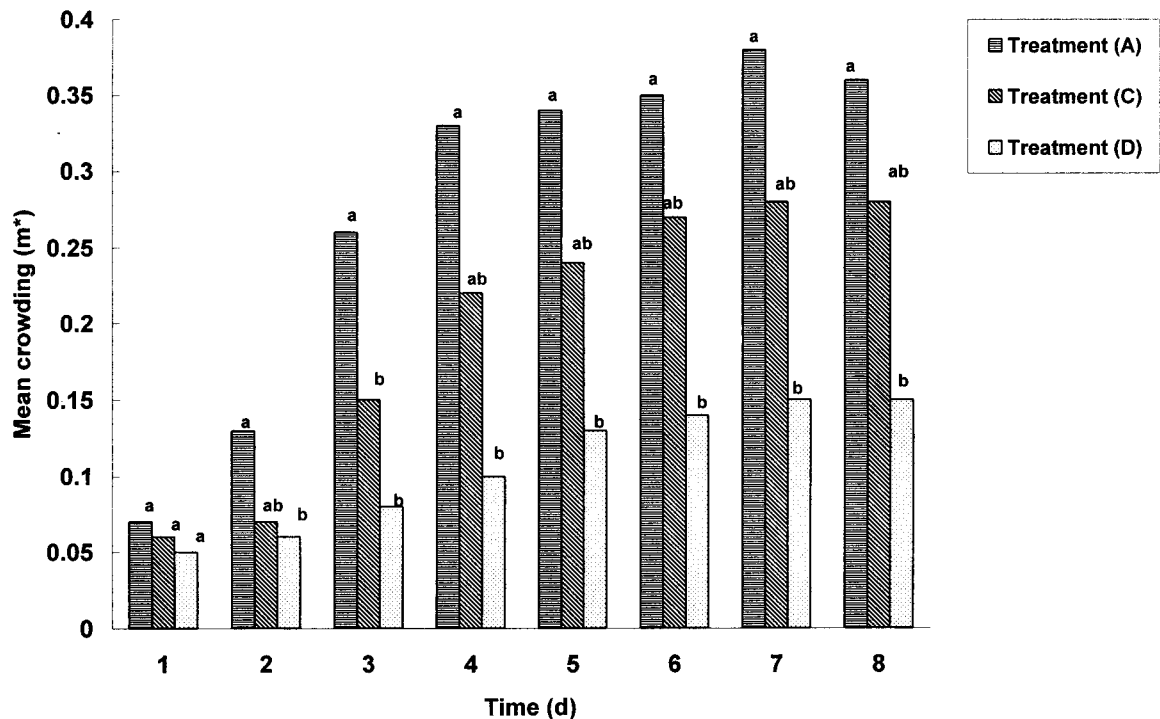
Fig. 1. Comparison of female egg dispersion behavior of *C. chinensis* when treated with different time schedules of providing males. There were significant differences in mean crowding of eggs on the 2<sup>nd</sup> day of the experiment (indicated by an asterisk, \*). Treatment B: one female was paired with one male and the male was discarded at the 9<sup>th</sup> hour; two virgin males were introduced on the 24<sup>th</sup> hour. Treatment C is the same as described in Table 1.

求偶的機率。相較之下，以控制雌蟲交尾次數的做法較屬於機制性的試驗，目的在於驗證雌蟲行多次交尾的利弊。本試驗處理則考慮雄蟲本身之存在以及其求偶干擾的作用，將雄蟲對產卵中雌蟲所可能造成的影響，包括對產卵數、產卵分布、以及壽命等生活史加以探討。

在不同供蟲時間處理下，可得知當產卵中雌蟲突然受到雄蟲求偶干擾時，其產卵行為會因而受到影響。雌蟲在試驗第 24 小時提供 2 隻雄蟲時(處理組 B)因受到雄蟲突然出現的求偶行為所造成的干擾(相較於在試驗開始時即以 2 隻雄蟲處理之雌蟲—處理組 C)，卵

平均擁擠度明顯上升，但在試驗第 3 天以後即與處理組 C 無顯著差異(圖一)。此結果顯示產卵中雌蟲在面臨雄蟲突然進來干擾時，可能因而改變其部分行為以因應雄蟲的求偶，但在一段時間之後，便已有良好的適應方式，使得產卵分布因而不再有差異。

根據圖一，雄蟲突然干擾所造成的影響是致使卵平均擁擠度上升，然而在不同的雄蟲密度處理下，單隻雌蟲組(處理 A)之卵平均擁擠度則顯著大於 4 隻雄蟲組(處理 D)(圖二)。亦即當完全沒有雄蟲存在時，雌蟲的產卵分布反而較不均勻。此結果顯示突然干擾的效應是存在的(平均擁擠度上升)，但在有



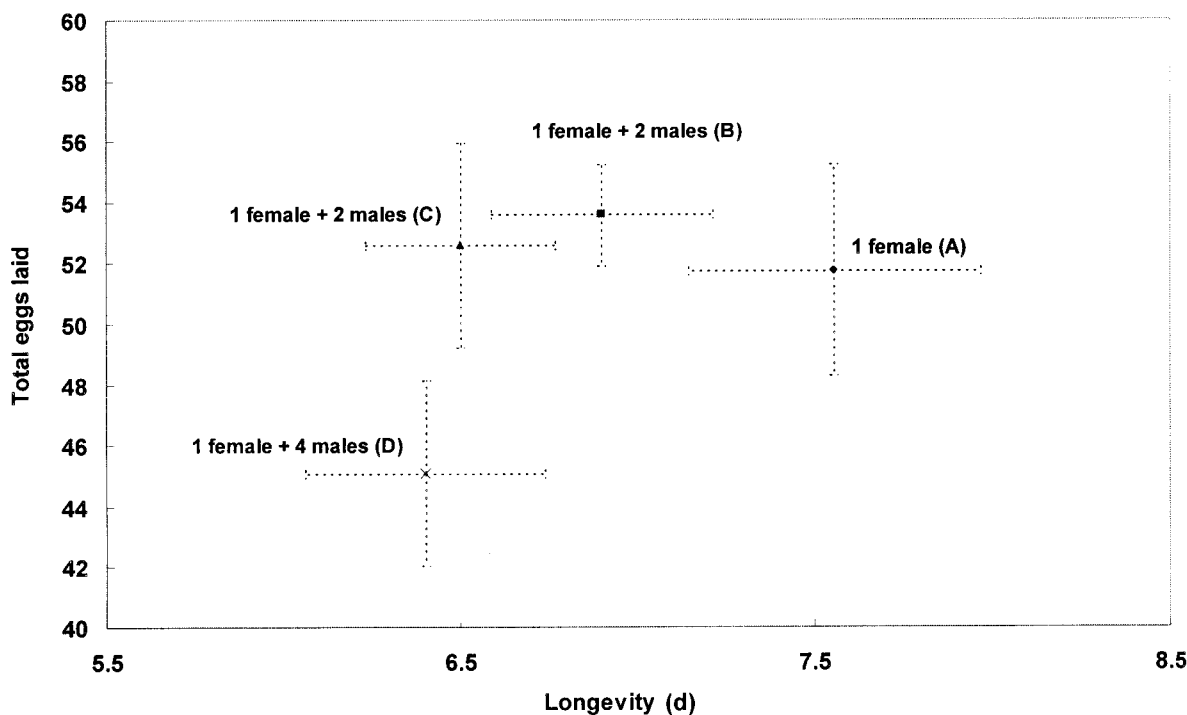
圖二 雄蟲密度對綠豆象雌蟲產卵擁擠度之影響。處理組說明如表一。

Fig. 2. Comparison of female egg dispersion behavior of *C. chinensis* when treated with different male numbers. There were significant differences in mean crowding of eggs. Treatments A, C, and D are the same as described in table 1. The same letter within the same day indicates no significant difference by unpaired *t*-test ( $p > 0.05$ ).

雄蟲持續存在的情況下，雌蟲反而產生適應性行為(平均擁擠度下降)。因此，平均擁擠度是否真正反映出雌蟲對寄主品質判別？我們在此提出兩種假說：1. 寄主豆品質有差異，並對子代適存值有嚴重影響。當一顆品質好的1卵豆價值高於品質差的0卵豆時，雌蟲在不受雄蟲干擾的情況下，可多花費時間在檢查寄主豆上。因此有的1卵豆被接受，有些0卵豆反而被拒絕，導致卵平均擁擠度高，因此平均擁擠度高並不意味著子代適存值較低。然而在多隻雄蟲處理組，由於雌蟲花費在拒絕雄蟲求偶，因而沒有足夠的時間分辨寄主豆的品質，而僅以豆上卵的有無當作優先判斷的指標，導致卵平均擁擠度反而較低，此時對子代適存值反而可能比較不利。

亦即，在無雄蟲處理組，雌蟲表現出對子代適存值較佳之行為，故以平均擁擠度來判斷子代適存值並不恰當。2. 寄主豆品質均勻，0卵豆的價值高於1卵豆。若雌蟲可以在很短的時間內判別寄主豆的品質，並且學習記憶之時，則因多隻雄蟲處理會導致雌蟲攀爬寄主豆的機率增高(Lan, unpublished)，雌蟲可能因此而對環境資源瞭解得更完備，造成產卵分布較均勻。

在生殖花費的研究上，一般認為生物會在壽命與生殖量上作權衡，亦即當生殖的子代數目多時，則壽命會降低，反之則壽命會增加。因此壽命和子代數應是呈負相關的(Lessells, 1991)。然而一些與生殖相關的因素常常會影響壽命，進而影響到子代數目。



圖三 雄蟲供蟲時間及密度對綠豆象雌蟲壽命及總產卵數之影響。處理組說明如表一及圖一。

Fig. 3. Comparison of trade-offs between longevity and total number of eggs laid by females of *C. chinensis* treated with different time schedules of providing males and different male numbers. Treatments A, B, C, and D are the same as described in table 1 and figure 1.

在本試驗中可清楚得知，2隻雄蟲處理組(處理組C)雖與單隻雄蟲處理組(處理組A)在產卵數上無異，其壽命卻顯著地減少，即雄蟲的干擾雖減少其壽命，卻未因此而減少其子代數，降低其適存值。但在4隻雄蟲處理組(處理組D)，不但壽命減少了，子代數亦減少。因此過多的雄蟲求偶干擾是有造成適存值降低的可能性。此一結果是否即為雌蟲適應性行為？亦即當雌蟲不拒絕雄蟲求偶，而不斷進行交尾，是否會造成壽命更短或子代數更少，則須進一步證實。

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# Effects of Male Interference on Oviposition Behavior of the Adzuki Bean Weevil, *Callosobruchus chinensis* (L.), (Coleoptera: Bruchidae)

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## ABSTRACT

Females of *Callosobruchus chinensis* (L.) produce a nearly uniform distribution of eggs on beans. This behavior results in minimizing larval competition within beans, and increasing the survival rate of larvae. Since the female behaves reluctantly after mating has occurred, the presence of a virgin male can induce solicitation behaviour which causes harassment to the female. Further, since females spend most of their time on oviposition and resting, the solicitation behavior of males therefore introduces interference to the oviposition behavior of the female. In this study, we manipulate differences in time schedules of offering virgin males and densities of virgin males to test the effects of male interference on egg dispersion behavior, total numbers of eggs laid, and longevity of females. The total numbers of eggs laid by females paired with four virgin males were significantly lower than those of females paired with one virgin male for 9 h. Therefore, a high density of virgin males, which introduced a high frequency of interference, resulted in decreasing fecundity of females. When offering virgin males with a different time schedule, females paired with two virgin males at the 24th hour from the beginning of the experiment showed significantly higher mean crowding on the 2<sup>nd</sup> day than did females paired with two virgin males at the beginning of the experiment, but there were no differences the day after. This result suggests that male solicitation behavior causes interference to female egg dispersion behavior, but the female immediately adapts after 1 d. Contrary to previous predictions, a high density of males did not result in an increase in the mean crowding of eggs. Females paired with one male for 9 h showed higher mean crowding from the 2<sup>nd</sup> day than did females paired with several males. The two levels of effects by manipulation of time scheduling and density of virgin males suggest that the effects of male harassment on fitness of offspring are complex and require further study. Comparison of trade-offs between longevity and total number of eggs laid by females suggests that females pairing with more males can cause reduction in both longevity and total number of eggs laid. Therefore, excessive male solicitation behavior can cause interference which can decrease fitness of the female.

**Key words:** bean weevil, male harassment, mean crowding, total eggs laid.