

棉铃虫温度依赖的生长发育及雌性先熟现象^{*}

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摘 要 在昆虫中,雄虫先于雌虫羽化,称为雄虫先熟现象,而雌虫先于雄虫羽化,称为雌虫先熟现象。前者最为普遍,后者报道较少。本试验在 20、22 和 25℃ 下对棉铃虫 *Helicoverpa armigera* (Hübner) 的生长发育进行了详细的研究。结果显示发育历期随温度的升高而缩短,雌雄间发育历期有着显著的差异,各个温度下雌虫均比雄虫先羽化,表明棉铃虫属于雌性先熟种类,而这种差异主要是由于雌虫的蛹期较短所致。幼虫发育历期与蛹重呈显著的正相关性。

关键词 棉铃虫, 发育历期, 蛹重, 雌性先熟

Temperature-dependent development and protogyny in *Helicoverpa armigera*

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Abstract Insects in which males emerge before females are protandrous whereas those in which females emerge before males are protogynous. The former are common but the latter are rare. The growth and development of the cotton bollworm, *Helicoverpa armigera* (Hübner), was systematically investigated at 20, 22 and 25°C. The results indicate that development time gradually shortened with increasing temperature and differed significantly between females and males. Females were protogynous; emerging before males at all three temperatures. Their earlier emergence was due to a shorter pupal duration. Pupal weight was positively correlated with the duration of larval development.

Key words *Helicoverpa armigera*, development duration, pupal weight, protogyny

在许多昆虫中,雌雄羽化时间常不同步。雄性比雌性先羽化称为雄性先熟(protandry),雌性比雄性先羽化则称为雌性先熟(protogyny)。在这 2 种羽化模式当中,雄性先熟在世代不重叠或“一夫一妻”制的昆虫种类中最为常见,例如多种蝴蝶和蛾类;而雌性先熟则较少见,报道也很少(Thornhill and Alcock, 1983; Buck, 2001)。

雌性先熟或者雄性先熟,统称为发育历期的性二型性。发育历期与昆虫的生长、发育以及繁殖等生活史特性直接相关。例如,一个短的幼虫期可以降低幼虫的死亡率(Roff, 1992; Stearns,

1992)。发育历期对昆虫的体型也有很大的影响,一个短的发育历期意味着小的体型;反之,长的发育历期将导致大的体型(Roff, 1992; Stearns, 1992)。雌雄间发育历期的差异也常常导致雌雄体型的差异(Nylin *et al.*, 1993; Brakefield and Mazzotta, 1995; De Block and Stoks, 2003; Mikolajewski *et al.*, 2005),即产生性体型的二型现象(sexual size dimorphism)。但无论对雌虫还是雄虫,体型大小都是非常重要的,因为一个大的体型意味着一个较高的繁殖力(Honek, 1993; Andersson, 1994; Blanckenhorn, 2000),而且可能增

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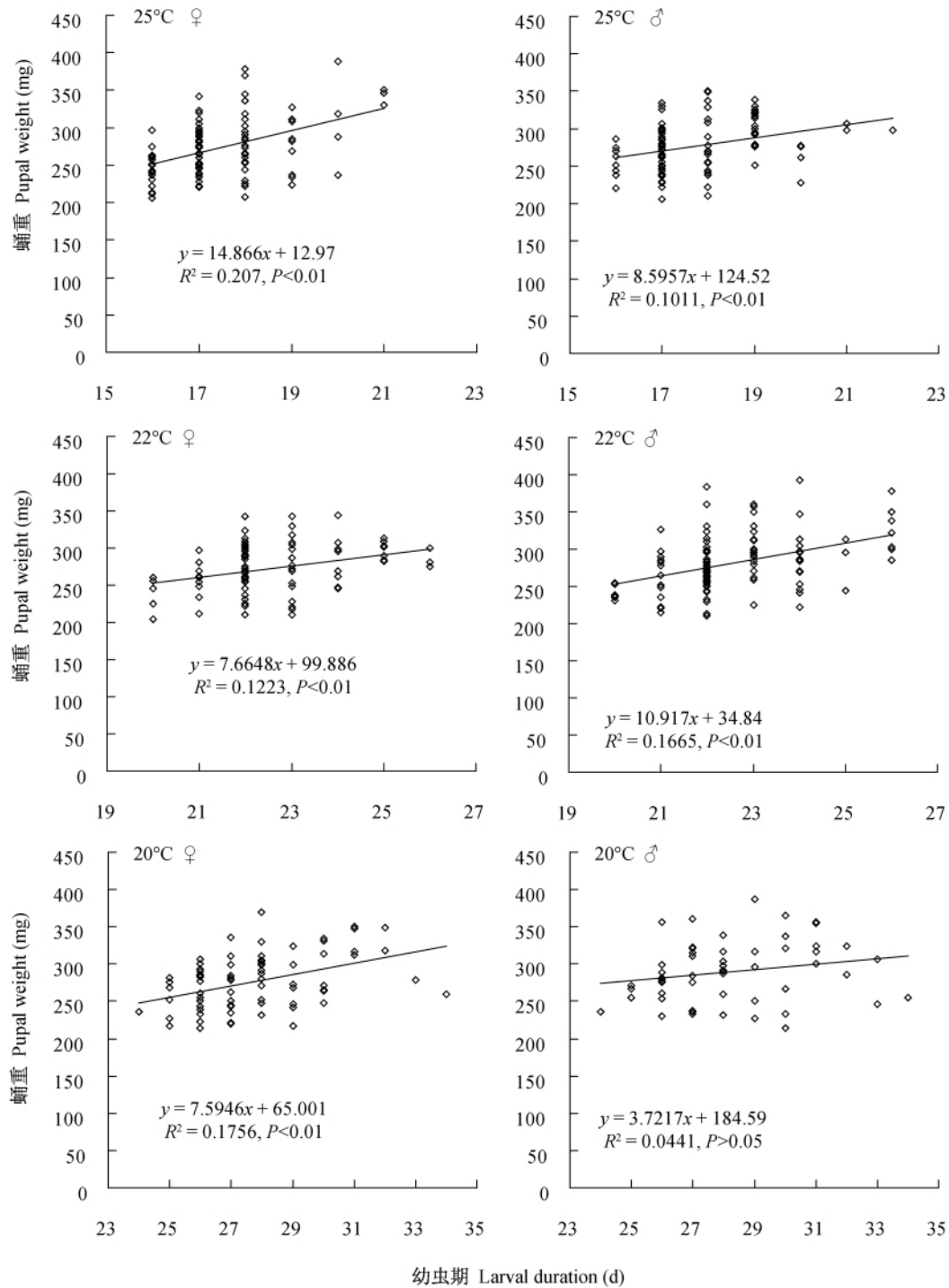


图 1 20、22 和 25℃, L:D=16:8 条件下幼虫期与蛹重的关系

Fig. 1 The relationship between larval duration and pupal weight under L:D=16:8 at 20, 22 and 25℃

差异 (20℃: $\chi^2 = 19.69$, $P < 0.05$; 22℃: $\chi^2 = 32.06$, $P < 0.05$; 25℃: $\chi^2 = 51.28$, $P < 0.05$)。从表 1 中可以看出,在不同温度下雌虫的总发育历期显著短于雄虫 ($P < 0.05$),在 20, 22

和 25℃下雌虫较雄虫分别短了 1.9、1.2 和 1.7 d,但雌雄间的幼虫期并没有差异 ($P > 0.05$),蛹期却存在显著的差异 ($P < 0.001$),表明蛹期的差异是导致雌性先羽化的主要原因。

表 1 在 20、22 和 25℃, L:D = 16:8 条件下雌雄的生活史数据 (平均值 ± 标准差)
Table 1 The life history data (mean ± SD) for females and males under L:D = 16:8 at 20, 22 and 25℃

	20℃		20℃		20℃	
	雌 Females (74)	雄 Males (58)	雌 Females (94)	雄 Males (112)	雌 Females (99)	雄 Males (95)
幼虫期 Larval duration (d)	27.8 ± 2.1a	28.2 ± 2.2a	22.7 ± 1.5b	22.6 ± 1.5b	17.5 ± 1.2c	17.8 ± 1.2c
蛹期 Pupal duration (d)	22.1 ± 1.6b	23.5 ± 1.4a	16.0 ± 1.7d	17.4 ± 1.1c	12.8 ± 1.0f	14.2 ± 0.9e
总发育历期 Total development period (d)	49.8 ± 2.7b	51.7 ± 2.7a	38.7 ± 2.4d	39.9 ± 2.0c	30.3 ± 1.7f	32.0 ± 1.5e
蛹重 Pupal weight (mg)	275.8 ± 37.4b	289.5 ± 39.8a	273.9 ± 31.9b	281.5 ± 39.1ab	272.9 ± 39.7b	277.3 ± 32.8b
发育速率 Growth rate (%)	30.7 ± 2.0a	30.5 ± 2.3a	37.5 ± 2.2b	37.8 ± 2.2b	48.0 ± 3.0c	48.7 ± 3.0c

注: 括号中为样本数, 同一行中不同字母表示差异显著 (one-way ANOVA 和 Duncan 多重比较, 差异显著水平 $P < 0.05$)。
The number of samples measured is in parentheses. Values in the same row followed by different letters are significantly different at 0.05 level based on one-way ANOVA and Duncan's multiple range test.

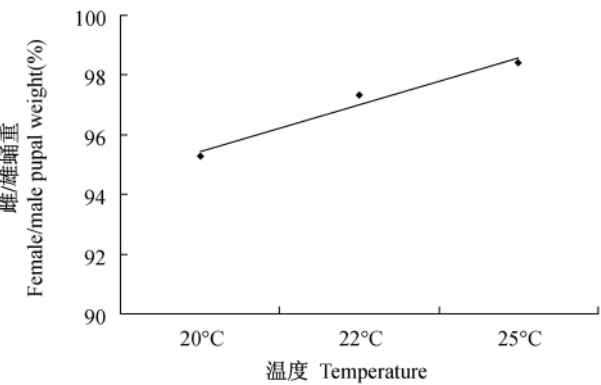


图 2 20、22 和 25℃ 下雌虫蛹重和雄虫蛹重的比值

Fig. 2 Quotient to female and male pupal weight at 20, 22 and 25℃

3 讨论

3.1 发育历期和发育速率对体型的影响

在很多动物种类当中, 不同性别间发育历期和发育速率的差异是与体型的性二型密切相关的 (Wiklund *et al.*, 1991; Leigh 1992; Shine 1994; Teather and Weatherhead, 1994; Wiklund and Fagerström, 1977)。有的因雌性的发育历期长, 从而导致性二型现象 (Mackey, 1978; Lederhouse *et al.*, 1982; Nylin *et al.*, 1993; Brakefield and Mazzotta, 1995; De Block and Stoks, 2003;

Mikolajewski *et al.*, 2005); 有的因性别间发育速率的差异导致体型的性二型 (Telang *et al.*, 2001; Yasuda and Dixon, 2002; Blanckenhorn, 2005)。当然, 有的是发育历期和发育速率都存在差异导致体型的差异 (Bradshaw and Holzapfel, 1996; Ernsting and Isaaks, 2002)。因此可以推断发育历期和发育速率可能都是影响体型的重要因素。在 20℃ 下, 棉铃虫雄虫的蛹重显著大于雌虫的蛹重 ($P < 0.05$), 但雄虫的发育速率是小于雌虫的 (雌虫: 30.7; 雄虫: 30.5), 因此较长的幼虫期 (蛹的重量主要在幼虫期获得) 可能是导致雄虫蛹重较大的主要原因。22 和 25℃ 下雄虫的蛹重也是大于雌虫蛹重的, 但并没有显著的差异, 然而雄虫无论是发育历期还是发育速率都是比雌虫更大的, 这些都有可能是导致雄虫蛹重更大的原因。我们的试验还表明, 温度的上升减小了性体型的二型性 (图 2), 这可能是随着温度的升高, 发育历期显著缩短, 发育速率显著增加, 导致了雌雄体重趋于平衡, 其生态意义值得探讨。

3.2 成虫羽化的雌性先熟现象

以上结果表明了棉铃虫是雌性先熟的昆虫种类, 雌性在 3 个温度下均显示出了较短的发育历期。但发育历期的差异并不是在整个发育阶段都表现的, 而是发生在蛹期, 在所有的温度下, 雌蛹的发育历期均短于雄蛹。因此, 雌性先熟是由于

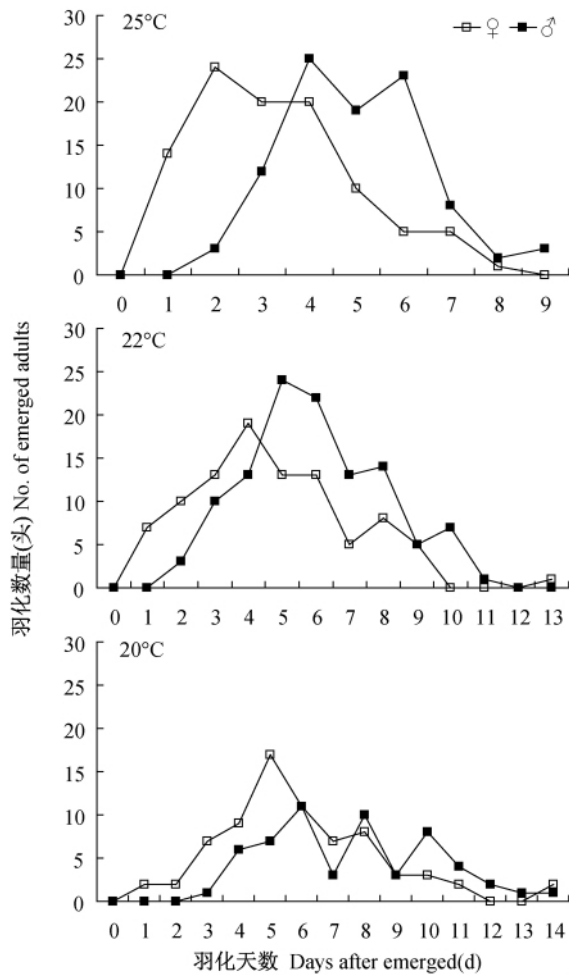


图3 20、22 和 25°C 每天羽化的雌雄虫的数量

Fig.3 Daily emergence of females and males *Helicoverpa armigera* at 20, 22 and 25°C

雌性蛹期较短导致的(表1)。在一些雌性先熟的种类当中,是由于短的幼虫期加上短的蛹期的共同作用造成的,例如哥斯达黎加的蓑蛾 *Oilketicus kirbyi*,正是由于雌虫比雄虫有较短的幼虫期及蛹期造成了雌虫先羽化(Stephens, 1962)。而果蝇 *Drosophila melanogaster* 和蚤蝇科一些种类雌性先熟的原因和棉铃虫一样,都是由于雌虫较短的蛹期,而不是幼虫期造成的(Bakker and Nelissen, 1963; Nunney, 1983; Buck, 2001),而且认为是由于精子的分化与成熟过程需要耗费更多的时间(Nunney, 1996)。但雄性先熟的一些种类却表现出一些不一样的现象,例如在多个昆虫种类中由于雌性幼虫期增加了一个龄期而导致了雄性先熟(Esperk *et al.*, 2007)。

雌性先熟与雄性先熟对不同的昆虫种类可能有着不同的意义,但必定对昆虫的繁殖产生重要的影响。但这种影响对不同昆虫种类可能是不同的,特别是当羽化时间增加了死亡的风险的时候,雌雄就应该缩小它们之间的差异(Wiklund and Fagerström, 1977; Singer, 1982; Bulmer, 1983; Iwasa *et al.*, 1983; Parker and Courtney, 1983)。在哥斯达黎加,蓑蛾的雌虫比雄虫先羽化,但雄虫只能存活 3 ~ 5 d,并且只能使有限的雌虫受精(Campos *et al.*, 1987),那么羽化时间则对繁殖有着很大的影响,雌雄应该尽量缩短它们之间的差异来增加交配的成功率。但如果该种昆虫的种类存在世代重叠,并且有着一个稳定的种群数量,那么羽化时间对繁殖的影响就完全不一样了。在田间,一般情况下棉铃虫存在大量个体,且个体间发育差异很大,存在明显的世代重叠,棉铃虫雌雄性成熟的差异不仅不影响田间的正常交配,且避免了近亲繁殖(Topper, 1987),因而对棉铃虫种群是有益的,在长期的进化过程中得以保存。而田间品系在室内饲养时交配率却很低,交配高峰期不相遇可能是一个重要的原因,即由于羽化时间的差异,当雄蛾交配高峰出现时,正是雌蛾拒绝交配的时候(Colvin *et al.*, 1994),而雌、雄最佳交配高峰期的相遇则是成功繁殖所必需的。从图2可以看出,棉铃虫的雌性的羽化高峰都相应的比雄虫提前了,就会有大量的个体可能因为羽化时间的差异而错过最佳的交配时间,这对避免近亲繁殖是有利的。在室内为了提高棉铃虫的交配成功率,可将雄蛹放入较高温度下以使雌、雄羽化同步,但是对于同一雌蛾产下的后代,采用这种方法会带来近亲繁殖的风险。为了提高卵孵化率和幼虫的成活率不宜采用这种方法,最佳的方法还是需要扩大种群数量,保证足够的不同来源的亲本和足够的同期羽化的雌雄个体。

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