



异律寄生蜂的寄主关系及其进化*

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摘要 异律寄生蜂 (Heteronomous parasitoids) 是指雌蜂、雄蜂卵及幼期分别对应不同的寄主关系和发育方式的寄生蜂。依据雌蜂、雄蜂卵及幼期所寄生的位置、所利用寄主种类和寄生方式的差异, 异律寄生蜂可划分为异位初寄生蜂、异主初寄生蜂和异律复寄生蜂。本文重点关注蚜小蜂 Coccophaginae 亚科的异律寄生蜂, 依据其雌蜂、雄蜂卵及幼期所对应的寄主关系、寄主种类和发育方式进行梳理与归类, 总结了异律寄生蜂的生殖方式和异律发育模式, 结合其生活史特性探讨了异律寄生蜂的寄主选择和适应性进化, 并辨析了异律寄生蜂在生物防治中的利弊与应用。

关键词 异律寄生蜂; 复寄生; 生殖特性; 进化; 生物防治

The evolution of heteronomous parasitoids

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Abstract Heteronomous parasitoids are species in which males have different host relationships than females. According to their host relationship and developmental pattern, heteronomous parasitoids are categorized as either diphagous, heterotrophic or heteronomous. In many species of the Coccophaginae, a subfamily of the Aphelinidae, the sexes have different hosts. In this review, we focus on heteronomous members of the Coccophaginae, categorize heteronomous parasitoids according to their host relationship and summarize the varying reproductive modes and developmental patterns of this group. We also review hypotheses on the evolution of heteronomous parasitoids based on current understanding of their life history. Finally, we discuss the controversial topic of using heteronomous parasitoids for biological control.

Key words heteronomous parasitoids; hyperparasitism; reproduction; evolution; biological control

寄生蜂是一类幼期营寄生生活的膜翅目 (Hymenoptera) 昆虫, 成虫将卵产于寄主体内或体外, 幼虫孵化后取食寄主内容物以补充营养。绝大多数情况下, 雌蜂、雄蜂卵及幼期利用同一种寄主, 两性间的寄生方式和发育方式并无差别, 即雌蜂、雄蜂卵及幼期具有相同的寄主关系 (Hunter and Woolley, 2001)。异律寄生蜂是寄生蜂中一个特殊的类群, 雌、雄个体分别对应不同的寄主关系 (Walter, 1983; Williams and

Polaszek, 1996; Hunter and Woolley, 2001)。这种膜翅目昆虫异律寄生的现象仅在蚜小蜂科 Aphelinidae, Coccophaginae 亚科的部分寄生蜂中观察到, 具体表现为雌蜂均为初级寄生蜂, 主要寄生蚜虫、粉虱和介壳虫等半翅目昆虫; 一小部分种的雄蜂同雌蜂一样, 初寄生于同种寄主, 但雌性卵和雄性卵被雌蜂分别产于寄主体内和体外; 另有一些种的雄蜂卵及幼期利用与雌蜂不同种的寄主, 初寄生于鳞翅目昆虫的卵; 更有多数

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种的雄蜂为复寄生蜂,其卵及幼期利用初级寄主体内的同种或异种寄生蜂幼蜂完成发育 (Hunter and Woolley, 2001)。

1 异律寄生蜂的归类

为了总结归纳异律寄生蜂与性别相关的寄主选择与发育特性,昆虫学家曾尝试从不同的角度对其进行划分 (Flanders, 1959, 1967; Zinna, 1961, 1962; Ferrière, 1966; Yasnosh, 1976; Walter, 1983)。本文基于 Walter (1983) 提出的划分体系,依据雌蜂、雄蜂卵被产于寄主的位置、所利用的寄主种类以及幼期的寄生方式将异律寄生蜂划分为三大类别:(1)雌蜂、雄蜂均为同一种半翅目昆虫的初级寄生蜂(即直接寄生植食性昆虫),雌性卵被产于寄主体内且雌性幼期营内寄生,而雄性卵被产于寄主体外且雄性幼期营外寄生,这一类雌蜂、雄蜂卵和幼期初寄生于同一种寄主的不同位置的寄生蜂,称为异位初寄生蜂 (Diphagous parasitoids);(2)雌蜂、雄蜂均为初级寄生蜂,雌性卵及幼期寄生于半翅目昆虫,

而雄性卵及幼期寄生于鳞翅目昆虫,这一类雌蜂、雄蜂初寄生于异种寄主的寄生蜂,称为异主初寄生蜂 (Heterotrophic parasitoids);(3)雌蜂为半翅目昆虫的初级寄生蜂,雄蜂卵及幼期复寄生于半翅目昆虫体内的同种或异种寄生蜂幼期(幼虫或蛹前期),为次级寄生蜂,这一类寄生蜂统称为异律复寄生蜂 (Heteronomous hyperparasitoids) (图 1)。在这里,被雌蜂卵和幼期寄生的半翅目昆虫被称为初级寄主,雄蜂卵和幼期所寄生的初级寄主内的寄生蜂则被称为次级寄主。

1.1 异位初寄生蜂

目前,已知的异位初寄生蜂主要存在于食蚧蚜小蜂属 *Coccophagus*。雌蜂、雄蜂均为蚧总科 Coccoidea 同种蚧虫的初级寄生蜂,雌成蜂将产卵器穿过蚧虫表面鳞片,把雌性卵产于寄主体内;将产卵器沿蚧虫鳞片下表面插入鳞片与叶面的交界处,把雄性卵产于寄主体表。这一类别包括 *Coccophagus bartletti* Annecke and Insley (Walter,

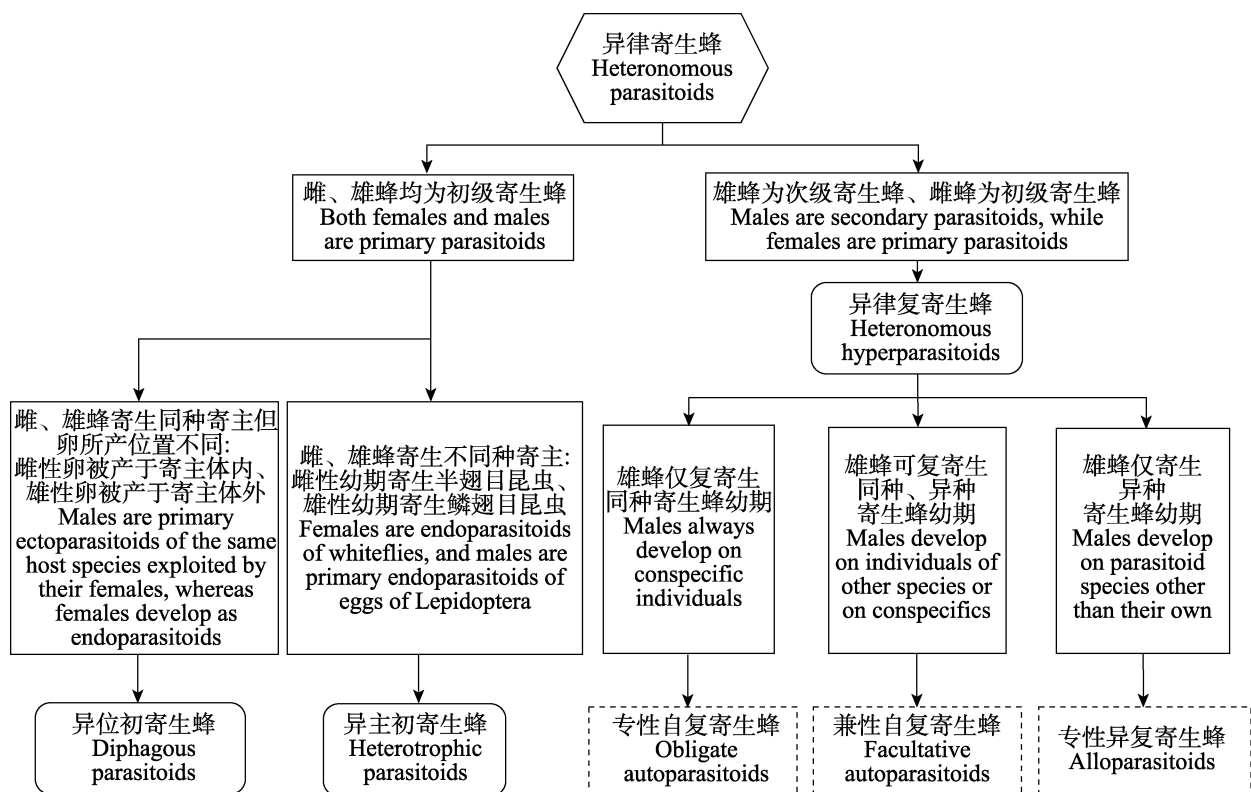


图 1 异律寄生蜂的寄主关系及归类 (改自 Walter, 1983)

Fig. 1 The host relationship and classification of heteronomous parasitoids (adapted from Walter, 1983)

1993)、*Coccophagus hemera* (Walker) (Zinna, 1961)、*Coccophagus longifasciatus* Howard (Flanders, 1959)、*Coccophagus ochraceus* Howard (Flanders, 1959)、*Coccophagus matsuyamensis* Ishihara (Viggiani, 1980)、*Coccophagus saissetiae* (Annecke and Mynhardt) (Mazzone and Viggiani, 1984) 和 *Coccophagus varius* (Silvestri) (Mazzone and Viggiani, 1984) 等。

1.2 异主初寄生蜂

异主初寄生蜂是异律寄生蜂中比较极端的类型。迄今为止, 确认到种的异主初寄生蜂仅有恩蚜小蜂属 *Encarsia* 的 *E. porteri* (Mercet), 其雌幼虫在烟粉虱若虫体内成功发育, 而雄幼虫可寄生于 5 种鳞翅目昆虫[黎豆夜蛾 *Anticarsia gemmatilis* (Hübner)、苹果蠹蛾 *Cydia pomonella* (Linnaeus)、美洲条螟 *Diatraea saccharalis* (Fabricius)、卷叶蛾毛虫 *Crociosema aporema* (Walsingham) 和麦蛾 *Sitotroga cerealella* (Oliver)] 的卵并成功羽化, 而在健康的烟粉虱若虫或被寄生的烟粉虱若虫上均未曾观察到有雄性卵和幼虫寄生并最终成功羽化 (Viscarret and Lopez, 2004)。

1.3 异律复寄生蜂

在异律寄生蜂中, 绝大部分属于异律复寄生蜂, 雄性卵及幼期寄生于次级寄主。异律复寄生特性现已在 *Coccophaginae* 亚科中的异角蚜小蜂属 *Coccobius*、类食蚜蚜小蜂属 *Coccophagoides*、食蚜蚜小蜂属 *Coccophagus*、恩蚜小蜂属 *Encarsia* 和四节蚜小蜂属 *Pteroptrix* 等中观察到 (表 1)。根据雄蜂所利用的次级寄主种类和雌蜂产雄卵时次级寄主的状态, 异律复寄生蜂还可进一步细分如下。

1.3.1 次级寄主的种类 根据雄蜂卵及幼期复寄生所利用的次级寄主的种类, 异律寄生蜂可进一步划分为三个类别 (图 1) (Walter, 1983): (1) 专性自复寄生蜂 (Obligate autoparasitoids): 仅以同种雌蜂 (幼期) 为次级寄主, 如 *Coccobius intermedius* Gahan (Flanders, 1967)、*Coccophagoides kuwanai* (Silvestri) (Flanders, 1960)、*Coccophagus*

baldassarii Compere (van den Bosch et al., 1955) 和日本恩蚜小蜂 *Encarsia japonica* Viggiani (李焱, 2009) 等至少 8 种; (2) 兼性自复寄生蜂 (Facultative autoparasitoids): 以同种或异种寄生蜂 (幼期) 为次级寄主, 如松突圆蚧花角蚜小蜂 *Coccobius azumai* Tachikawa (钟景辉, 2009)、*Coccophagoides similis* Masi (Zinna, 1962)、*Coccophagus atratus* Compere (Donaldson and Walter, 1991a, 1991b)、*Encarsia aleuroilicis* Viggiani (Viggiani, 1987) 和东方四节蚜小蜂 *Pteroptrix orientalis* (Silvestri) (Viggiani and Garonna, 1986) 等至少 30 种; (3) 专性异复寄生蜂 (Alloparasitoids): 仅以异种寄生蜂 (幼期) 为次级寄主, 如 *Coccophagus basalis* Compere (Flanders et al., 1961)、*Coccophagus* sp. nr. *gurneyi* Compere (Abeeluck and Walter, 2019)、*Coccophagus malthusi* Girault (Annecke and Insley, 1974) 和 *Lounsburyia trifasciata* Compere (Hunter and Woolley, 2001) 等至少 4 种。值得注意的是, 兼性自复寄生蜂和专性异复寄生蜂中的部分小蜂 (表 1), 可以利用姬小蜂科 Eulophidae、跳小蜂科 Encyrtidae 和金小蜂科 Pteromalidae, 甚至广腹细蜂科 Platygasteridae 及蚜茧蜂科 Aphididae 的寄生蜂作为次级寄主, 次级寄主范围不局限于蚜小蜂科 Aphelinidae 的近缘种属。

1.3.2 次级寄主的可利用性 根据雌成蜂产雄性卵时次级寄主的可利用情况, 异律复寄生蜂可划分为两个类别: (1) “直接” 异律复寄生蜂: 雌成蜂将雄性卵直接产在寄生于初级寄主体内的次级寄主体内或体表 (Walter, 1983)。绝大多数异律寄生蜂属于此类别, 包括食蚜蚜小蜂属 *Coccophagus* 的大部分种、花角蚜小蜂属 *Coccobius*、类食蚜蚜小蜂属 *Coccophagoides* 和恩蚜小蜂属 *Encarsia* (Hunter and Woolley, 2001)。(2) “间接” 异律复寄生蜂: 雌成蜂将雄性卵产在初级寄主体内, 直到同种或异种初级寄生蜂在发育中将初级寄主的营养消耗至尽并形成干燥环境后, 雄性卵才会孵化。雄性卵在次级寄主暂时缺失或不可利用期间保持静态的现象被称为 “受抑孵化” (Inhibited hatch) (Hunter and

表 1 蚜小蜂科主要异律复寄生蜂
Table 1 The main heteronomous hyperparasitoids in Aphelinidae

异律复寄生蜂 Heteronomous parasitoids	初级寄主 [#] Primary hosts [#]	异种次级寄主 Secondary hosts	参考文献 References
专性自复寄生蜂 Obligate autoparasitoids			
花角蚜小蜂属 <i>Coccobius</i>			
<i>Coccobius intermedius</i> Gahan	盾蚧科: 褐圆蚧 <i>Chrysomphalus aonidum</i> (Linnaeus)	*	Flanders, 1967
类食蚧蚜小蜂属 <i>Coccophagoides</i>			
<i>Coccophagoides kuwanai</i> (Silvestri)	盾蚧科: 桑盾蚧 <i>Pseudaulacaspis pentagona</i> (Targioni-Tozzetti)	*	Flanders, 1960
<i>Coccophagoides utilis</i> Doutt	盾蚧科: 橄榄片盾蚧 <i>Parlatoria oleae</i> (Colvee)	*	Broodryk and Doutt, 1966
食蚧蚜小蜂属 <i>Coccophagus</i>			
<i>Coccophagus baldassarii</i> Compere	蜡蚧科: 油橄榄蜡蚧 <i>Saissetia oleae</i> Bern	*	van den Bosch et al., 1955
绒食蚧蚜小蜂 <i>Coccophagus gossypariae</i> Gahan	毡蚧科: <i>Gossyparia spuria</i> (Modeer)	*	Viggiani, 1999
黄盾食蚧蚜小蜂 <i>Coccophagus semicircularis</i> (Frster)	蜡蚧科: 米兰褐软蚧 <i>Coccus hesperidum</i> Linnaeus	*	Viggiani, 1984
恩蚜小蜂属 <i>Encarsia</i>			
日本恩蚜小蜂 <i>Encarsia japonica</i> Viggiani	粉虱科: 烟粉虱 <i>Bemisia tabaci</i> (Gennadius)	*	李焱, 2009
欧甫恩蚜小蜂 <i>Encarsia opulenta</i> (Silvestri)	粉虱科: 桔黑刺粉虱 <i>Aleurocanthus woglumi</i> Ashby	*	Nguyen, 2004
兼性自复寄生蜂 Facultative autoparasitoids			
花角蚜小蜂属 <i>Coccobius</i>			
松突圆蚧花角蚜小蜂 <i>Coccobius azumai</i> Tachikawa	盾蚧科: 松突圆蚧 <i>Hemiberlesia pitysophila</i> Takagi	Y	钟景辉, 2009
<i>Coccobius debachi</i> Compere & Annecke	盾蚧科: 白轮盾蚧属 <i>Aulacaspis tegalensis</i> (Zhnt.)	Y	Williams, 1972
<i>Coccobius seminotus</i> Silvestri	盾蚧科: 白轮盾蚧属 <i>Aulacaspis tegalensis</i> (Zhnt.)	蚜小蜂科: 花角蚜小蜂属 <i>Coccobius subflavus</i> Silvestri; 跳小蜂科: 阿德跳小蜂属 <i>Adelencyrtus miyarai</i> Tachikawa; 姬小蜂科: 啮小蜂属 <i>Tetrastichus</i> spp.	Williams, 1977
<i>Coccobius subflavus</i> Annecke & Insley	盾蚧科: 白轮盾蚧属 <i>Aulacaspis tegalensis</i> (Zhnt.)	蚜小蜂科: 花角蚜小蜂属 <i>Coccobius seminotus</i> Silvestri	Williams, 1972
牡蛎蚧蚜小蜂 <i>Coccobius testaceus</i> Masi	盾蚧科: 桤柳白盾蚧 <i>Adiscodiaspis tamaricola</i> Malenotti	Y	Flanders, 1967

续表 1 (Table 1 continued)

异律复寄生蜂 Heteronomous parasitoids	初级寄主 [#] Primary hosts [#]	异种次级寄主 Secondary hosts	参考文献 References
类食蚧蚜小蜂属 <i>Coccophagoides</i>			
<i>Coccophagoides similis</i> (Masi)	盾蚧科: 梨圆蚧 <i>Diaspidiotus perniciosus</i> Comstock	蚜小蜂科: 花角蚜小蜂属 <i>Coccobius</i> spp. 类食蚧蚜小蜂属 <i>Coccophagoides</i> spp.	Zinna, 1962
食蚧蚜小蜂属 <i>Coccophagus</i>			
<i>Coccophagus atratus</i> Compere	蚧科: <i>Filippia gemina</i> de Lotto	蚜小蜂科: 食蚧蚜小蜂属 <i>Coccophagus</i> spp. 跳小蜂科: 阔柄跳小蜂属 <i>Metaphycus</i> spp.	Donaldson and Walter, 1991a, 1991b
<i>Coccophagus capensis</i> Compere	蜡蚧科: 油橄榄蜡蚧 <i>Saissetia oleae</i> Bern	¥	Flanders, 1967
黑蚧南美蚜小蜂 <i>Coccophagus caridei</i> (Brèthes)	蜡蚧科: <i>Coccus viridis</i> (Green)	¥	Flanders, 1967
<i>Coccophagus cowperi</i> Girault	蜡蚧科: 咖啡绿蚧 <i>Coccus viridis</i> (Green), 咖啡盔蚧 <i>Saissetia coffeae</i> (Walker)	¥	Flanders, 1967
<i>Coccophagus eleaphilus</i> Silvestri	蜡蚧科: 油橄榄蜡蚧 <i>Saissetia oleae</i> Bern	蚜小蜂科: 食蚧蚜小蜂属 <i>Coccophagus</i> spp.	van den Bosch <i>et al.</i> , 1955
<i>Coccophagus eritreaensis</i> Compere	软蚧科: 桔黑软蚧 <i>Coccus pseudomagnoliarum</i> (Kuwana)	蚜小蜂科: 食蚧蚜小蜂属 <i>Coccophagus</i> spp.	van den Bosch <i>et al.</i> , 1955
<i>Coccophagus gurneyi</i> Compere	粉蚧科: 嗜桔粉蚧 <i>Pseudococcus calceolariae</i> (Maskell)	¥	Parkes and Walter, 2001
赖食蚧蚜小蜂 <i>Coccophagus lycimnia</i> Walker	蜡蚧科: 日本球蚧 <i>Eulecanium kunoensis</i> Kuwana	蚜小蜂科: 食蚧蚜小蜂属 <i>Coccophagus</i> spp. 跳小蜂科: 阔柄跳小蜂属 <i>Metaphycus</i> spp.	Schweizer <i>et al.</i> , 2002
<i>Coccophagus nigratus</i> Compere	蜡蚧科: 油橄榄蜡蚧 <i>Saissetia oleae</i> Bern	¥	Flanders, 1967
<i>Coccophagus pseudococci</i> Compere	粉蚧科: 桔棘粉蚧 <i>Pseudococcus citriculus</i> Risso	¥	Flanders, 1959
<i>Coccophagus rusti</i> Compere	蜡蚧科: 油橄榄蜡蚧 <i>Saissetia oleae</i> Bern	¥	Flanders, 1959
恩蚜小蜂属 <i>Encarsia</i>			
<i>Encarsia aleuroilicis</i> Viggiani	粉虱科: <i>Aleuroviggianus adrianae</i> Iaccarino	广腹细蜂科: 无脉细蜂属 <i>Amitus</i> spp. 姬小蜂科: 木虱啮小蜂属 <i>Tetrastichus</i> spp. 跳小蜂科: 木虱跳小蜂属 <i>Psyllaephagus</i> spp.	Viggiani, 1987
双斑恩蚜小蜂 <i>Encarsia bimaculata</i> (Heraty and Polaszek)	粉虱科: 烟粉虱 <i>Bemisia tabaci</i> (Gennadius)	¥	Antony <i>et al.</i> , 2004
<i>Encarsia clypealis</i> (Silvestri)	粉虱科: 桔黑刺粉虱 <i>Aleurocanthus woglumi</i> Ashby	¥	Flanders, 1959

续表 1 (Table 1 continued)

异律复寄生蜂 Heteronomous parasitoids	初级寄主 [#] Primary hosts [#]	异种次级寄主 Secondary hosts	参考文献 References
<i>Encarsia lahorensis</i> (Howard)	粉虱科: 柑橘粉虱 <i>Dialeurodes citri</i> (Ashmead)	¥	Hudson and Williams, 1986
露狄恩蚜小蜂 <i>Encarsia lutea</i> (Masi)	粉虱科: 烟粉虱 <i>Bemisia tabaci</i> (Gennadius)	蚜小蜂科: 桉角蚜小蜂属 <i>Eretmocerus mundus</i> Mercet	Awadalla <i>et al.</i> , 2014
<i>Encarsia noyesi</i> Hayat	粉虱科: <i>Aleurodicus dugesii</i> Cockerell	¥	Schoeller <i>et al.</i> , 2018
硕恩蚜小蜂 <i>Encarsia pergandiella</i> Howard	粉虱科: 烟粉虱 <i>Bemisia tabaci</i> (Gennadius)	蚜小蜂科: 恩蚜小蜂属 <i>Encarsia formosa</i> Gahan, 桉角蚜小蜂属 <i>Eretmocerus mundus</i> Mercet	Bográn and Heinz, 2002
梨园蚧蚜小蜂 <i>Encarsia perniciosi</i> Tower	盾蚧科: 梨圆蚧 <i>Quadraspidiotus perniciosus</i> (Comstock)	¥	Stouthamer and Luck, 1991
<i>Encarsia scapeata</i> Rivnay	粉虱科: <i>Trialeurodes lauri</i> Signore	¥	Gerling <i>et al.</i> , 2009
斯氏恩蚜小蜂 <i>Encarsia smithi</i> (Silvestri)	粉虱科: 桔黑刺粉虱 <i>Aleurocanthus woglumi</i> Ashby	蚜小蜂科: 恩蚜小蜂属 <i>Encarsia opulenta</i> (Silvestri)	Nguyen and Sailer, 1987
浅黄恩蚜小蜂 <i>Encarsia sophia</i> (Girault & Dodd)	粉虱科: 烟粉虱 <i>Bemisia tabaci</i> (Gennadius)	蚜小蜂科: 丽蚜小蜂 <i>Encarsia formosa</i> Gahan, 桉角蚜小蜂属 <i>Eretmocerus eremicus</i> Rose & Zolnerowich, <i>Eretmocerus hayati</i> Zolnerowich & Rose	Collier and, Hunter, 2001; Yang <i>et al.</i> , 2012; 刘林州等 2013
三色恩蚜小蜂 <i>Encarsia tricolor</i> Förster	粉虱科: 甘蓝粉虱 <i>Aleyrodes proletella</i> (Linnaeus)	蚜小蜂科: 丽蚜小蜂 <i>Encarsia formosa</i> Gahan	Berks, 1991
四节蚜小蜂属 <i>Pteroptrix</i>			
东方四节蚜小蜂 <i>Pteroptrix orientalis</i> (Silvestri)	盾蚧科: 桑盾蚧 <i>Pseudaulacaspis pentagona</i> (Targioni-Tozzetti)	¥	Viggiani and Garonna, 1986
专性异复寄生蜂 Alloparasitoids			
食蚧蚜小蜂属 <i>Coccophagus</i>			
<i>Coccophagus basalis</i> Compere	蜡蚧科: 米兰褐软蚧 <i>Coccus hesperidum</i> Linnaeus	跳小蜂科: 阔柄跳小蜂属 <i>Metaphycus stanleyi</i>	Flanders <i>et al.</i> , 1961
<i>Coccophagus</i> sp. nr. <i>gurneyi</i> Compere	粉蚧科: 马缨丹绵粉蚧 <i>Phenacoccus parvus</i> Morrison	跳小蜂科: 长索跳小蜂属 <i>Anagyrus diversicornis</i> (Howard)	Abeeluck and Walter, 2019
<i>Coccophagus malthusi</i> Girault	蜡蚧科: 蜡蚧属 <i>Ceroplaste</i> spp.	¥	Annecke and Insley, 1974
<i>Lounsburyia</i>			
<i>Lounsburyia trifasciata</i> (Compere)	蜡蚧科: 油橄榄蜡蚧 <i>Saissetia oleae</i> Bern	蚜小蜂科: 食蚧蚜小蜂属 <i>Coccophagus</i> spp.	Hunter and Woolley, 2001

专性自复寄生蜂: 雄蜂仅以同种雌蜂作为次级寄主; 兼性自复寄生蜂: 雄蜂以同种或异种寄生蜂作为次级寄主; 专性异复寄生蜂: 仅以异种寄生蜂作为次级寄主; #代表此处为文献中报导最多的初级寄主, 初级寄主范围可能不限于此; *代表利用同种幼蜂作为次级寄主, 未见报道可利用异种次级寄主; ¥: 代表未明确异种次级寄主。

Obligate autoparasitoids: Males always develop on conspecific larvae; Facultative autoparasitoids: Males develop on individuals of heterospecific species or on conspecifics; Alloparasitoids: Males always develop on heterospecific parasitoids; # indicates the primary hosts listed here are the ones reported in literature; * indicates males develop on conspecific larvae; ¥ indicates the heterospecific hosts are not clear.

Woolley, 2001)。已报道的这一类别寄生蜂包括 *C. basalis* Compere (Flanders *et al.*, 1961)、*C. pseudococci* Compere (Flanders, 1959)、*Lounsburyia trifasciata* Compere (Hunter and Woolley, 2001)、*C. gurneyi* (Parkes and Walter, 2001) 以及东方四节蚜小蜂 *Pteroptrix orientalis* (Silvestri) (Viggiani and Garonna, 1986)。其中, 食蚜蚜小蜂属 *C. basalis* 的雄性卵和雌性卵均被产在蚧科 *Coccoidea* 褐软蚧 *Coccus hesperidum* Linnaeus 或珠蜡蚧属蚧虫 *Saissetia* spp. 的食道下神经节内, 雄性卵被产在阔柄跳小蜂属寄生蜂 *Metaphycus* spp. (异种初级寄生蜂) 消耗完初级寄主的液体内融物后孵化, 之后雄性幼虫摄食初级寄主完成自身发育; 在雄卵静止 (未发育) 期间, 卵周围形成一层黑色的外膜, 可以保护它免受初级寄生蜂幼虫的攻击, 同时防止同种雌性幼虫的寄生 (Flanders *et al.*, 1961)。

2 异律寄生蜂的生殖与发育

2.1 生殖方式

膜翅目昆虫的性别决定为单双倍体决定, 二倍体雌性发育自受精卵, 单倍体雄性发育自未受精卵, 即为产雄孤雌生殖 (Hunter and Woolley, 2001)。已交配的雌成蜂在产卵过程中通过一定的机制控制卵是否受精, 进而产生雄性或雌性后代 (Yang *et al.*, 2012)。对异律寄生蜂而言, 雌成蜂根据不同类别的寄主产下相应性别的后代。

值得注意的是, 异律寄生蜂的一些物种存在孤雌产雌品系, 这种生殖方式一般是通过沃尔巴克氏菌 *Wolbachia* 和胞内共生菌 *Cardinium* 介导, 相对于两性品系而言, 孤雌产雌品系与性别相关的寄主选择或发育特性发生了变化 (Hunter, 1999)。例如, 异律复寄生蜂 *E. tabacivora* 感染胞内共生菌的孤雌产雌品系, 雌成蜂不区分初级和次级寄主, 将未受精卵 (发育为单性生殖雌性后代) 随机产于初级和次级寄主, 产于初级寄主的无性雌性卵得以顺利发育; 即带胞内共生菌的孤雌生殖品系的未交配雌蜂的产卵行为, 类似于两性生殖品系的已交配雌蜂 (Zchori-Fein *et al.*,

2001; Kenyon and Hunter, 2007; Giorgini *et al.*, 2009)。还有极个别的异律寄生蜂为产两性孤雌生殖, 如东方四节蚜小蜂 *P. orientalis*, 未交配的雌成蜂在白桃盾蚧体内同时产雌、雄卵, 雄蜂为间接异律复寄生蜂, 幼期雄蜂延迟发育, 复寄生先行发育的幼期雌蜂 (Garonna, 1990)。

2.2 与性别相关的异律发育

异律寄生蜂由于雌性和雄性卵分别产于不同的寄主或同一寄主的不同位置, 因此, 异律寄生蜂存在幼期发育条件和形态特征上的性别差异。以异律复寄生蜂为例, 偶见雌成蜂将受精/未受精卵产在不相应的寄主上, 卵无法孵化或极个别卵孵化但随即死亡, 说明雌雄幼期发育受相应寄主条件限制 (Gerling, 1966; Williams, 1972; Gerling *et al.*, 1987; Hunter, 1993, 1999)。雌雄性卵均由雌蜂卵巢孕育并排出体外, 内寄生雌雄蜂卵未见明显差异, 均为卵圆形, 而外寄生雄性卵见报道有缠绕或卷曲的卵柄 (Ding *et al.*, 1995; Williams, 1972; Walter, 1983), 推测是用于将卵子附着在宿主上 (Walter, 1983) 或防止水分流失 (Hunter and Woolley, 2001)。雌蜂可能使用腺体分泌物来区分雄性和雌性卵子, 其中雌卵是胞囊化的, 而雄卵是不胞囊化的 (Walter, 1983)。此外, 雄卵发育位置可能并不固定, 次级寄主偏大, 雄卵可能内寄生, 次级寄主过小, 雄卵可能外寄生 (Parkes and Walter, 2001)。说明成年雌蜂对两性卵的不同处理方式可能造成后代形态差异。雌雄蜂功能性气门数量随龄期发育而变化, 液体环境中的低龄内寄生蜂气门不明显, 而干燥环境下的外寄生蜂 (雄蜂) 1 龄雄性幼虫的气门比成熟雌性幼虫的气门要大, 且雌蜂、雄蜂高龄幼虫气门数也不尽相同 (Fisher, 1961; 钱明惠等, 2007a)。Pedata 等 (2003) 报道, 一些恩蚜小蜂的胚外膜能释放出畸形细胞, 可抑制寄主的免疫功能, 自复寄生蜂双斑恩蚜小蜂的雌性胚胎发育中发现了胚外膜的存在 (钱明惠等, 2007b), 但其是否具有免疫功能还有待确认。此外, 在蚜小蜂胚胎发育中发现, 硕恩蚜小蜂的极体不消解, 发育成一个被称

为滋养羊膜的环绕胚胎多倍体层,滋养羊膜可能也有抑制寄主免疫的功能(钱明惠等, 2007a, 2007b)。在异养寄生蜂 *Encarsia porteri* 中观察到滋养羊膜包围着发育中的雌性胚,而雄性则没有(Hunter *et al.*, 1996),雌雄蜂生理结构的差异也可能是导致其异律发育的原因。此外,在 *E. hispida* 中发现,无性雌性卵能够在次级寄主上成功发育,这种突破复寄生蜂雌、雄异律的发育条件限制的情况,仅在此一种异律寄生蜂中被观察到(Giorgini *et al.*, 2009)。

3 异律寄生蜂进化史

3.1 基于生活史的假说

由于分类鉴定需使用雌蜂作为标准,在不同的寄主中对应异律寄生蜂雄蜂并厘清关系非常困难,蚜小蜂的系统分类尤其是涉及异律寄生特性的寄生蜂系统发育树的建立还存在极大的分歧(Misof *et al.*, 2014; Peters *et al.*, 2017)。基于异律寄生蜂在昆虫中集中出现于蚜小蜂这一分支,普遍认为异律寄生特性源自独立的进化事件,并提出了诸多基于生活史特性的异律寄生演化的假说,如“间接复寄生起源”(Flanders, 1967)、“雌雄异位寄生起源”(Walter, 1993)和“竞争驱动的内复寄生起源”(Hunter and Woolley, 2001)等。不过不同假说的观点及其争论与分歧,难以通过具体的案例得以验证和解决,因此,至今仍未形成相对成熟的假说理论(Pennacchio and Strand, 2006; Hayward *et al.*, 2011)。下面我们重点阐述几个相关的经典假说。

Flanders (1967) 从寄主资源限制的角度考虑,提出间接复寄生起源的进化路径:传统寄生蜂-间接异律复寄生蜂-直接异律复寄生蜂-异位初寄生蜂和异主初寄生蜂。该路径的第一步,从传统寄生蜂到间接异律复寄生蜂,在认为聚寄生特性为祖先特性的情况下更为适用,在同一寄主中,雄性通过延迟孵化获得相对于其姐妹的竞争优势(Rojas-Rousse *et al.*, 1999)。食蚜蚜小蜂属 *C. basalis* 和 *C. gurneyi* 雌成蜂将卵产在寄主的食道下神经节中,雄卵延迟孵化,待雌性幼虫

将寄主的内容物摄取殆尽形成干燥环境后,雄卵再行孵化,此时寄主体内的幼期雌蜂是雄蜂发育的营养来源(Flanders, 1967)。间接复寄生起源在寄主资源限制及初级寄主大多已被寄生的情况下似乎有可能发生(Williams, 1977; Viggiani, 1984)。不过,质疑的观点认为成年雄蜂卵及幼虫本可以在初级寄主上发育,自然选择为什么要保留雄蜂卵必须等到初寄生蜂发育后才孵化的形式(Walter, 1993)?一些相关的观点认为异律复寄生涉及群体选择,即自复寄生可随着寄主发生动态调节自身种群密度,在寄主数量充足的情况下,更多的繁育雌性后代以扩大种群密度;在环境条件不适宜的情况下,利用雄性后代的发育来制约种群数量的发展(Flanders, 1959; Zinna, 1962; 孙丽影等, 2014)。然而,这些论点并不能直接解释异律复寄生雄对寄主的选择性优势。

Zinna (1961) 依据成年雌蜂寄主搜索范围的扩大提出雌、雄异位寄生起源的推测:传统寄生蜂-异位初寄生蜂-异律复寄生蜂-异主初寄生蜂。首先,雌成蜂将雌性卵和雄性卵均产于同一种寄主,在超寄生条件下,产在寄主体外的雄性后代获得竞争优势,适应性发育进化为异位初寄生蜂;为了种群繁衍,雌成蜂繁殖策略升级,采取不同的寄主接受标准产两性后代,雄性后代通过寄生竞争对手从而压制竞争者完成发育,进化出异律复寄生蜂;最后,雌成蜂的繁殖策略进一步进化,将雌雄后代分别产于不同种类的寄主,发育为异主初寄生蜂。传统寄生蜂到异位初寄生蜂是进化路线中的第一步的推测,源自于对以下案例的观察:传统寄生蜂印巴黄蚜小蜂 *Aphytis melinus* 和岭南黄蚜小蜂 *A. lingnanensis* 的雌、雄蜂卵及幼虫均是初级外寄生蜂,但成年雌性通常会在寄主身体的不同部位产卵,将雌卵产在身体上部,而将雄卵产在身体下部(Luck *et al.*, 1982)。雌成蜂对雌性卵和雄性卵的不同处理,导致在进化过程中雌性和雄性幼虫的发育是解耦的,Walter (1993) 认为生态环境适应性是导致异位初寄生蜂的起源,同时,竞争因素在异律寄生蜂的进化起源过程中应该发挥重要作用;他

进一步指出, 如果雌、雄异位寄生作为一种竞争策略出现, 那么在异位初寄生蜂中, 外寄生的雄性后代相对于内寄生的雌性后代应该更具竞争优势。这一竞争优势尚未得到实验证实。此外, 有观点质疑异位初寄生蜂种群的普遍性, 鉴于该特性目前仅存在于食蚜蚜小蜂属(Williams and Polaszek, 1996; Hunter and Woolley, 2001)。

Hunter 和 Woolley (2001) 认为寄主体内寄生蜂幼虫的种内竞争和种间竞争在进化中占据重要位置, 进而提出竞争驱动的内复寄生起源: 即单寄生性的初级内寄生蜂-异律复寄生蜂(兼性异律复寄生蜂-专性异律复寄生蜂)-异位初寄生蜂-异主初寄生蜂, 其中, 雄性后代外寄生的异律复寄生蜂向初级寄生蜂发生进化逆转, 进化出异位初寄生蜂, 最后进化出异主初寄生蜂。

Hunter 和 Woolley (2001) 认同 Walter (1983) 的观点, 认为相较于雄蜂而言, 雌蜂的寄主关系是相对保守的, 内寄生很可能是一种祖先状态。接下来, 从传统的内寄生蜂进化到异律复寄生蜂这一步, Hunter 和 Woolley (2001) 探讨了起源于聚寄生的可能性, 指出虽然聚寄生蜂的雄性通过延迟孵化可以获得相对于姐妹雌蜂的竞争优势, 从而具有演化为外寄生的间接复寄生蜂的可能性, 但由于聚寄生蜂在蚜小蜂中极为少见, 故否定了聚寄生起源的假定。从单寄生起源角度考虑, 在田间寄主限制条件下, 单寄生性雌蜂可能会在同一寄主上反复产卵(超寄生), 假设雌蜂超寄生时倾向于产下雄性卵, 鉴于雄性适合度与寄主体型大小的关联弱于雌性(Charnov *et al.*, 1981; Charnov, 1987), 且在一些种类中雄性卵比同期产下的雌性卵更早孵化进而获得竞争优势(Field *et al.*, 1997), 就有可能出现雌蜂接受或拒绝已寄生寄主产雄性卵的选择压力。一旦雌蜂接受已寄生寄主产雄, 接下来的问题就是, 雄蜂能否成功发育? 一般来说, 在膜翅目寄生蜂中, 内竞争的结果取决于第一次产卵和第二次产卵之间的时间间隔, 低龄和高龄的寄生蜂幼虫都可能获胜(Visser *et al.*, 1992; Marris and Casperd, 1996)。在低龄寄生蜂幼虫具有竞争优势的类食蚜蚜小蜂属 *Coccophagine* spp. 中, 如果

后寄生的雄蜂幼期利用先寄生的寄生蜂发育, 雄蜂就有可能发育为兼性自复寄生蜂(Hunter and Woolley, 2001)。一旦雄性发育成复寄生蜂, 那么雄性将会在初级寄生蜂和次级寄生蜂之间进行权衡, 考虑到寄主的高度利用, 自然选择很可能倾向于发育为复寄生蜂的雄性, 进而从兼性自复寄生蜂最终转变为专性自复寄生蜂(Hunter and Woolley, 2001)。值得注意的是, 上述关于异律寄生特性演化的推测, 不同的观点间具有很大的分歧, 目前都还停留在推论的阶段尚未通过具体的案例得以验证, 至今仍未形成相对成熟的假说理论(Pennacchio and Strand, 2006; Hayward *et al.*, 2011)。

3.2 进化转折与进化维持

蚜小蜂的发育受环境条件、寄主数量与质量等因素的影响(Williams and Polaszek, 1996)。我们可以推测, 由于某些因素的改变, 蚜小蜂科 Aphelinidae 祖先物种的一个分支中首先出现雌蜂、雄蜂发育解耦现象, 雌蜂、雄蜂发育独立进行。随着该分支谱系的增多, 雌蜂、雄蜂异律发育形式多样化, 上述关于异律寄生演化的推测, 多认为异律复寄生蜂是由传统寄生蜂向异律寄生蜂进化迈出的第一步。

进化转折: 雌成蜂产雄对“错误/非常规”寄主的选择是决定异律复寄生能否发生的关键因素。寄生蜂主要通过化学信息物质搜索、定位其栖境并寄主(Tan and Liu, 2014), 对于幼虫寄生蜂而言, 主要依赖于寄主与植物互动时释放的化学物质(Inbar and Gerling, 2008)。烟粉虱寄生蜂的寄主定位能力研究表明, 相对于其他几种初级寄生蜂, 复寄生蜂(硕恩蚜小蜂)能最快定位到被烟粉虱感染的寄主(Heinz and Parrella, 1998); 此外, 烟粉虱和蚜虫常同域发生, 且蚜虫的发生高峰期一般早于烟粉虱(Tan *et al.*, 2014), 烟粉虱寄生蜂(如浅黄恩蚜小蜂和丽蚜小蜂)可利用蚜虫侵染植株所释放的化学物质定位栖境(Tan and Liu, 2014)。定位寄主后, 寄生蜂需要做出是否接受寄主的行为决策, 受到寄主环境的状态(寄主资源丰富度、寄主质量及栖

境的大小和结构等)与雌蜂的状态(抱卵量、交配经历等)等因素影响(Hoffmeister and Roitberg, 1997; Zhang *et al.*, 2015)。寄主资源受限条件下,合理的寄主处理策略是接受遇到的所有寄主(Yang *et al.*, 2012),在三色恩蚜小蜂和浅黄恩蚜小蜂中均观察到雌蜂在低寄主相遇率下不拒绝任何寄主的现象(Hunter and Godfray, 1995; Xu *et al.*, 2013)。由于寄生蜂是单双倍型性别决定方式,雌成蜂可以在交配后通过选择性受精来控制后代的性别(Visser *et al.*, 2014)。研究者推测在寄主资源受限雌蜂接受所有寄主情况下,偏好于在高质量的寄主上产雌,而将雄卵产于低质量的寄主(Hunter and Woolley, 2001)。这一推测主要基于雄蜂的繁殖适合度受寄主质量影响的程度小于雌蜂的假定(Desneux *et al.*, 2012)。在间接异律复寄生蜂中,雄蜂的发育需要初级寄生蜂消耗掉部分寄主,形成适合的空间后,雄蜂才开始发育。食蚜蚜小蜂属 *C. basalis* 成年雌蜂将雄卵和雌卵均产在蚜虫的食道下神经节内,雄卵只有在阔柄跳小蜂属寄生蜂(初级寄生蜂)完全消耗掉初级寄主的液体内融物后才孵化出来(Flanders, 1967)。假设成年雌蜂偏好于在个体更大的初级寄主上繁育雌性后代,而雌性后代在发育过程中不能消耗足够的寄主资源来刺激间接寄生的雄性卵的孵化。此时,雌蜂“错误”的产卵行为恰巧为雄性后代的发育找到适宜的寄主并顺利发育,那么这一物种很可能演化为异寄生蜂。

进化维持:目前报道的蚜小蜂科 Aphelinidae 物种中,绝大多数具有雌、雄异律发育特性(Hunter and Woolley, 2001)。基于异律寄生特性在膜翅目昆虫中集中出现于蚜小蜂这一分支,普遍认为异律复寄生特性源自独立的进化事件。无论是什么原因导致了异律的起源,维持它的因素肯定是极其强烈的。Hunter 和 Woolley(2001)探讨了异律生活史的维持是由于主动选择还是缺乏遗传变异。成年雌蜂对不同资源的产卵选择可能导致雌蜂、雄蜂发育不同期,尤其对于异律复寄生蜂而言,成年雌蜂需利用次级寄主产雄,这使得在生长季早期或新生境中,异律复寄生蜂

建立种群的难度提高,后代性比偏雌;在这种情况下,自然选择应该倾向于保留能够利用初级寄主产雄的雌蜂突变体才合理。此外,如果考虑 trade-off 的重要性,比如在次级寄主上所发育雄蜂与在初级寄主上所发育雄蜂的适合度差异,或许是维持异律寄生的因素,但此推测无法进行实证。结合上述,一方面,目前还没有主动选择的有力证据来支持异律寄生特性的维持;另一方面,缺乏遗传变异,尤其缺乏雄性幼虫在初级寄主体内发育的相关能力,这更有可能是维持异律寄生特性的重要因素。在对异律寄生蜂长达 80 余年的研究中,未异律复寄生蜂雄蜂在初级寄主上成功羽化的报道(Hunter and Woolley, 2001);即便偶见异律复寄生蜂雌蜂将未受精卵产在初级寄主上,后代也不能存活,如未交配的 *C. rusti* 雌蜂在初级寄主体内偶产下雄性卵,但解剖发现其发育至 1 龄幼虫不久后便死亡(Flanders and Herbert, 1969)。因此,解析制约雌幼虫和雄幼虫在相应的初级和次级寄主上的发育机制和遗传基础,将有助于我们了解异律寄生蜂进化过程中的转折与维持。

4 结语与展望

随着害虫抗药性的增加以及人们对环境健康的要求使得生物防治成为一条行之有效并能持续控害的途径。异律寄生蜂由于特殊的寄主关系和生殖方式使其受到关注,而关注的焦点多在于异律复寄生蜂与初级寄生蜂的种内与种间竞争(Xu *et al.*, 2013, 2016)。雄性后代在种群繁衍中必不可少,为产生雄性后代,异律复寄生蜂需寄生同种或异种寄生蜂,也就是说,1 头雄蜂的羽化意味着要牺牲 1 头雌蜂。这种特性在寄生蜂种群发展与害虫防控中是一把双刃剑。通过建立自复寄生蜂浅黄恩蚜小蜂多生境间迁移寄生蜂-寄主稳态的数学模型,发现相对于初级寄生蜂,自复寄生蜂与寄主间的稳态更不容易受到寄主种群增长的扰动,尤其是当寄生蜂可以在具有不均衡性的生境间迁移时(Huang *et al.*, 2016)。此外,一些学者提出,在自然生态群落中,兼性自复寄生蜂可能比初级寄生蜂更具优势,当兼性

自复寄生蜂与其它初级寄生蜂共存于同一生境时,成年雌蜂偏好在异种次级寄主上繁育雄性后代,可供雄蜂发育的寄主范围增加,异律复寄生蜂种群随之扩大(Zang *et al.*, 2011)。在有限寄主资源和丰富寄主资源条件下,对 1 种初级寄生蜂海氏桨角蚜小蜂与 1 种兼性复寄生蜂浅黄恩蚜小蜂的种间和种内竞争作用的研究表明,2 种寄生蜂之间存在复寄生、过寄生和取食已寄生寄主的竞争机制(Xu *et al.*, 2013),并且 2 种寄生蜂间竞争干涉作用的优势和强度受到寄主密度的影响(Xu *et al.*, 2016)。值得注意的是,即便存在竞争,复寄生蜂与初级寄生蜂的组合释放在寄主资源利用及寄生蜂种群动态的稳定性等方面比单种蜂释放更具优势(刘林州等, 2013; Xu *et al.*, 2015; 张晓明等, 2018),这可能与 2 种寄生蜂的种间和种内竞争水平差异有关。因此,对于兼性自复寄生蜂而言,寄生蜂在异种次级寄主上的高度适合性暗示其不但可以自行调节种群密度、维持寄主和寄生蜂种群动态稳定,而且能够在自然条件下与竞争对手共存(Avilla and Copland, 1987),增强生物防治效果。

此外,在生物防治过程中,异律寄生蜂的防治效果常常被低估。部分异律复寄生蜂属卵谐产类寄生蜂,通过取食寄主体液,以提供花粉、花蜜和昆虫蜜露等所不具备的必要营养,进而促进体内卵子成熟(Zang and Liu, 2009)。例如,兼性自复寄生蜂浅黄恩蚜小蜂因寄主取食导致烟粉虱若虫的死亡率达 59.7%,与寄生引起的寄主死亡数量相当(Zang and Liu, 2008)。还有一种常被忽略的隐藏的生防机制,寄生蜂刺死寄主但未成功产卵或其后代没能成功发育的非生殖效应(Abram *et al.*, 2019)。例如,兼性自复寄生蜂匀鞭蚜小蜂成年雌蜂在产卵前进行寄主检测,向寄主体内插入产卵器以评估寄主的适合性,与此同时向寄主体内注射杀卵剂或杀幼虫剂,杀死竞争者的后代,为同种后代营造适宜的发育环境(Hunter and Woolley, 2001)。在这个过程中,可能涉及到抑制寄主免疫系统的毒液、畸形细胞及多分 DNA 病毒等免疫因子,寄生蜂可能会拒绝在不适宜的寄主上产卵,或者在产卵

前被捕食者、寄主防御行为、竞争对手或其他非生物因素干扰而产卵失败(Abram *et al.*, 2019)。由于在研究寄生蜂对寄主生物防治效应时往往忽略掉上述因素,因此,异律寄生蜂的防效在实际生产中应高于预估值。

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