

# 中国寄生蜂研究及其在害虫生物防治中的应用\*

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**摘 要** 寄生蜂是一类重要的寄生性天敌昆虫, 种类繁多、习性复杂, 在害虫生物防治和综合治理中发挥着极其重要的作用。在产卵时, 寄生蜂携带的毒液、多 DNA 病毒等寄生因子就会随之进入寄主体内, 发挥调控寄主生长、发育、免疫、代谢、行为的作用, 从而保障了寄生蜂后代的发育。本文主要针对我国寄生蜂的系统分类、资源普查、生物学、生态学、寄主调控、人工繁殖、释放应用、田间保护和助增等方面的基础研究和应用进行了概述和整理。

**关键词** 生物防治; 寄生蜂; 资源多样性; 寄生因子; 寄主互作; 人工繁殖; 释放应用

## Review of research on parasitoids and their use in biological control in China

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**Abstract** Parasitoids are among the most important natural enemies of insect pests and are widely used as biological control agents in integrated pest management. In addition to their eggs, parasitoids inject several parasitoid-associated factors, such as venom and polydnvirus, into their hosts which alter the hosts development, immunity, metabolism and behavior. This paper reviews progress in research on the taxonomy, ecology, host regulation, mass rearing, field release, conservation and augmentation, of parasitoids in China over the past several decades.

**Key words** biological control; natural enemy; parasitoid; species diversity; biology; ecology; parasitoid-associated factor; host regulation; mass rearing; release; conservation; augmentation

我国利用天敌昆虫开展生物防治害虫的历史悠久, 早在公元前 304 年我国南方就有应用捕食性天敌黄猢蚁 *Oecophylla smaragdina* Fabr. 防治柑橘害虫的记录, 这是国际上“以虫治虫”最早记录。1932-1933 年祝汝佐率先在杭州田间释放桑螵卵寄生蜂控制桑螵危害, 这是我国首次释放寄生蜂控制害虫的试验 (祝汝佐, 1934)。20

世纪 50 年代初, 蒲蛰龙等成功利用赤眼蜂控制了甘蔗螟虫的为害 (朱涤芳等, 1992)。寄生蜂, 即寄生性膜翅目昆虫, 作为一类重要的天敌昆虫, 在我国害虫防治过程中发挥了重要的作用, 近几十年无论在基础研究, 还是在田间应用方面都取得了较大的发展, 本文就此进行简要的总结和回顾。

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# 1 寄生蜂的分类和资源发掘

## 1.1 寄生蜂的分类研究

早在 20 世纪 30 年代,我国最早从事寄生蜂分类研究的祝汝佐先生就发表了一系列寄生蜂资源调查的论文,如《杭州稻苞虫寄生蜂之考察》、《中国松毛虫寄生蜂志》等(赵修复,1991)。随后,胡经甫、赵修复、何俊华等分类学家对我国寄生蜂物种多样性进行了阶段性的记录和整理,如在《中国昆虫目录》(1941)中第一次对我国寄生蜂种类进行了汇总,《天敌昆虫图册》(1978)是常见天敌识别的工具书,在很大程度上促进了我国天敌昆虫特别是寄生蜂资源的调查(赵修复,1991)。20 世纪 80 年代后,我国的寄生蜂分类研究工作得到了很好的发展,表现为研究学者数量增多、涉及类群增多,研究生将寄生蜂的分类作为的论文选题内容。

建国以来寄生蜂分类工作就发现和记述的寄生蜂物种多样性可以简单概括如下。姬蜂总科 Ichneumonoidea 中记述姬蜂科 Ichneumonidae 489 属 2 125 种、茧蜂科 321 属 2 124 种(Yu *et al.*, 2016)。小蜂总科 Chalcidoidea 中记述蚜小蜂科 Aphelinidae 16 属 242 种、小蜂科 Chalcididae 16 属 70 种、跳小蜂科 Encyrtidae 126 属 483 种、姬小蜂科 Eulophidae 63 属 388 种、旋小蜂科 Eupelmidae 9 属 56 种、金小蜂科 Pteromalidae 114 属 452 种、棒小蜂科 Signiphoridae 2 属 4 种以及赤眼蜂科 Trichogrammatidae 38 属 173 种(Noyes, 2019)。在细蜂总科 Proctotrupoidea 中记述 5 科 24 属 407 种,包括细蜂科 19 属 365 种;柄腹细蜂科 1 属 9 种;窄腹细蜂科 2 属 30 种;离颚细蜂科和修复细蜂科均为 1 属 1 种(何俊华和许再福,2015)。在钩腹蜂总科 Trigonaloidea 中记述 8 属 45 种(Chen *et al.*, 2014; Tan *et al.*, 2017)。在旗腹蜂总科 Evanioidea 中记述旗腹蜂科 Evanioidea 5 属 18 种(Deans *et al.*, 2018)、举腹蜂科 Aulacidae 2 属 25 种(Chen *et al.*, 2016a)、褶翅蜂科 Gasteruptionidae 1 属 32 种(Zhao *et al.*, 2012; Tan *et al.*, 2016a)、冠蜂总科 Stephanoidea 6 属 27 种(Tan *et al.*, 2018)。在青蜂总科 Chrysidoidea 中记述短节蜂科

Sclerogibbidae 2 属 3 种(Liu and Xu, 2013)、犁头蜂科 Embolemyidae 2 属 8 种(Xu *et al.*, 2012)、肿腿蜂科 Bethyridae 10 属 104 种(Azevedo *et al.*, 2018)和螫蜂科 Dryinidae 16 属 190 种(Olmi and Xu, 2015)。

## 1.2 寄生蜂的资源发掘

以分类研究为基础,有针对性地开展不同农业生态体系中寄生蜂物种资源多样性的调查,为保护和利用本地寄生蜂天敌资源以及开展害虫生物防治和综合治理提供了基础资料。

重要害虫全国范围内寄生蜂资源多样性:小菜蛾 *Plutella xylostella* (Linnaeus) 的寄生性天敌(包括引进的在内)有 109 种,其中卵期寄生蜂 5 种、幼虫期寄生蜂 81 种、蛹期寄生蜂 23 种(陈宗麒等,2001);斜纹夜蛾 *Spodoptera litura* (Fabricius) 的寄生蜂有 40 种,其中原寄生蜂 29 种、重寄生蜂 11 种(何俊华等,2002);烟粉虱 *Bemisia tabaci* (Gennadius) 的寄生蜂共计 74 种,其中恩蚜小蜂属 *Encarsia* 47 种、桨角蚜小蜂属 *Eretmocerus* 24 种、埃宓细蜂属 *Amitus* 2 种及新姬小蜂属 *Neochrysocharis* 1 种(王继红等,2011);竹林主要害虫竹瘿广肩小蜂 *Aiolomorpha rhopaloides* Walker 的寄生蜂有 9 种(何孙强等,2016)。

重要害虫地区性寄生蜂资源多样性:北京地区舞毒蛾的寄生性天敌共计 17 种,其中卵期的天敌大蛾卵跳小蜂 *Ooencyrtus kuwanae* (Howard)、舞毒蛾卵平腹小蜂 *Anastatus disparis* (Ruschka)、幼虫期的绒茧蜂、斑痣悬茧蜂 *Meteorus pulchricornis* (Wesmael)、寄蝇类等,蛹期的寄蝇、广大腿小蜂 *Brachymeria lasus* Walker、舞毒蛾黑瘤姬蜂 *Coccygomimus disparis* (Viereck)、脊腿囊爪姬蜂 *Theronia atalantae* (Thunberg) 等(冯继华等,1999);福建省柑桔矢尖蚧 *Unaspis yanonensis* (Kuwana) 的寄生性天敌有 6 种,其中矢尖蚧蚜小蜂 *Aphytis yanonensis* DeBach *et Rosen* 和簇盾蚧黄蚜小蜂 *Aphytis unaspidis* Rose *et Rosen* 为优势种(龚建军等,1999);粉虱的寄生蜂有 22 种,其中蚜小蜂科 Aphelinidae 的恩蚜小蜂属 *Encarsia* 19 种和桨角蚜小蜂属

*Eretmocerus* 2 种、广腹细蜂科 *Platygastridae* 的 *Amitus* 属 1 种 (黄建等, 2000); 广东地区稻田生态系统中褐飞虱 *Nilaparvata lugens* (Stål) 卵寄生蜂有 20 种, 其中缨小蜂科 11 种、赤眼蜂科 9 种 (毛润乾等, 1999); 青海省云杉母树林害虫的寄生性天敌有 54 种, 其中云杉球果小卷蛾 *Pseudotomoides strobilellus* Linnaeus 上的曲姬蜂 *Scambus* sp.、马尾姬蜂 *Megarhyssa* sp. 和球果平胸姬小蜂 *Hyssopus nigritulus* (Zetterstedt) 为 3 种主要种 (汪有奎等, 2000); 浙江省茶树害虫黑刺粉虱 *Aleurocanthus spiniferus* (Quaintance) 上的寄生蜂有 8 种 (王义平等, 2001); 昆明地区瘤大球坚蚧 *Eulecaium gigantea* (Shinji) 的寄生有 6 种, 即球蚧花角跳小蜂 *Blastothrix sericea* (Dalman)、绵蚧阔柄跳小蜂 *Metaphycus pulvinariae* (Howard)、夏威夷食蚧蚜小蜂 *Coccophagus hawaiiensis* Timberlake、白蜡虫花翅跳小蜂 *Microterys sericari* Ishii、食蚧蚜小蜂 *Coccophagus* sp. 等 (陶玫等, 2002)。类似同样进行过寄生蜂调查的还有昆明的桔绵蜡蚧 *Chloropulvinaria aurantii* (Cockerell) (陈国华等, 2003)、红蜡蚧 *Ceroplastes rubens* Maskell (陶玫等, 2003b)、白生盘蚧 *Crescoccus candidus* Wang (陶玫等, 2003a)、分瓣臀凹盾蚧 *Phenacaspis kentiae* Kuwama (黄燕辉等, 2004)、浙江杭州地区的潜叶蝇 (Chen *et al.*, 2003)、烟粉虱 (杨帆等, 2016)、竹篦舟蛾 *Loudonta dispar* Kiriakof 和竹卵圆蝽 *Hippotiscus dorsalis* (Stål) (郭瑞等, 2016)、宁波地区的小菜蛾 (皇甫伟国等, 2010); 江淮棉区的棉大卷叶螟 *Sylepta derogata* Fabricius (康晓霞等, 2006)、新疆的温室白粉虱 *Trialeurodes vaporariorum* (Westwood) (柳斌等, 2009)、东疆玉米地叶蝉科害虫 (伊龙等, 2013)、玛纳斯国家湿地公园大青叶蝉 *Tettigella viridis* Linnaeus (林思雨等, 2016)、福建省的烟粉虱 (黄建等, 2010)、冀西北农牧交错区草地螟 *Loxostege sticticalis* L. (康爱国等, 2015)、宁夏的麦蚜 (刘军和等, 2014)、北方麦田的蚜虫 (Yang *et al.*, 2017a) 和棉蚜 *Aphis gossypii* Glover (Yang *et al.*, 2017b) 等。

作物生态系统中寄生蜂资源多样性: 稻田系

统中有 16 科 67 种以上寄生蜂、毗邻杂草中有 19 科 96 种 (毛润乾等, 2000; 李志胜等, 2002; 徐敦明等, 2004), 基本上是稻田害虫的初寄生蜂、少数为重寄生蜂; 新疆棉田茧蜂种类有 9 种, 其中麦蛾柔茧蜂 *Habrobracon hebetor* Say、中红侧沟茧蜂 *Microplitis mediator* Haliday、地老虎长体茧蜂 *Macrocentrus collaris* Spinola、瓢虫茧蜂 *Dinocampus coccinellae* Schrenk、燕麦蚜茧蜂 *Aphidius evenae* Haliday 为优势种 (吐尔逊·阿合买提等, 2006)。进行过类似调查的作物生态系统还有云南的酸甜石榴园 (吴海波等, 2009)、北京地区的梨园 (张学昌等, 2014)、湖北柑橘园 (郑文艳等, 2016) 等。

## 2 寄生蜂的生物学

### 2.1 幼蜂发育

对寄生蜂幼蜂的发育研究主要集中于卵 (胚胎发育过程中形态特征变化描述) 和幼虫龄期划分上。黄腹潜蝇茧蜂 *Opius caricivora* Fischer 整个幼期在 25 °C 条件下约需 327 h, 卵在产后 46-52 h 孵化, 幼蜂发育可分成 5 个龄期 (1 龄 22-23 h、2 龄 24 h、3 龄 10-14 h、4 龄 4-6 h 和 5 龄 20-26 h); 其中 1 龄幼蜂孵化后体外仍有卵膜包裹并具较发达的上颚、5 龄幼蜂口器下颚须之间出现了一个新的结构 “Transverse sclerite” (Xu *et al.*, 2007)。产入亚洲玉米螟 *Ostrinia furnacalis* (Guenée) 幼虫体内的腰带长体茧蜂 *Macrocentrus cingulum* Brischke 卵的发育历程为 10 min 开始卵裂、1 d 从卵壳中释放初级胚胎并分裂产生能形成桑葚胚的二级胚胎、3 d 从胚外膜中释放出来的二级胚胎进入胚胎发育阶段、6 d 胚胎发育进入胚带期、8 d 头尾形成、9 d 分节, 之后幼蜂出胚外膜 (即孵化)、13 d 后幼蜂从寄主体内钻出 (胡建等, 2008)。类似研究还有川硬皮肿腿蜂 *Scleroderma sichuanensis* Xiao (申莉莉和周祖基, 2002)、日本柄瘤蚜茧蜂 *Lysiphlebus japonicus* (Ashmead) (Gan *et al.*, 2003)、双斑侧沟茧蜂 *Microplitis bicoloratus* Xu *et al.* (Luo *et al.*, 2007)、管氏肿腿蜂 *Scleroderma guani* Xiao *et al.* (代平礼和徐志强, 2007)、菜

蛾盘绒茧蜂 *Cotesia vestalis* (Haliday) (Yu *et al.*, 2008; 原建强等, 2008)、半闭弯尾姬蜂 *Diadegma semiclauseum* (Hellén) (原建强等, 2008; Huang *et al.*, 2009a)、菜蛾啮小蜂 *Oomyzus sokolowskii* (Kurdjumov) (王春艳等, 2011)、颈双缘姬蜂 *Diadromus collaris* (Gravenhorst) (Zhao *et al.*, 2014)、东方蝗卵蜂 *Scelio orientalis* Dodd (刘婷等, 2009)、长尾全裂茧蜂 *Diachasmimorpha longicaudata* (Ashmead) (邵屯等, 2008)、平腹小蜂 *Anastatus* sp. (陈业林和利翠英, 1985)、中红侧沟茧蜂 (秦启联等, 2000a)。在把握寄生蜂胚胎期和幼蜂期发育动态的同时, 对在体外条件下培养寄生蜂胚胎以及幼蜂进行了探索 (胡建和刘峰, 2008), 发现了如整合素  $\beta$  亚基等能参与寄生蜂 (腰带长体茧蜂) 幼期发育调控 (胚胎增殖能力呈正相关) 的功能基因 (颜曦等, 2013)。

## 2.2 寄主选择

容性内寄生蜂 (Koinobiont endoparasitoid) 为了保证后代发育, 母代雌蜂会依据简单食性理论, 选择产卵于营养质量较高的寄主, 并决定产何种性别的卵, 同时雌蜂产卵时还考虑了子代蜂的繁殖力。菜蛾啮小蜂寄生小菜蛾幼虫时并没有对寄主发育龄期表现出明显的偏好性, 子代雌蜂体内怀卵量不随寄主个体的大小变化, 只随着产卵次数的增加而呈线性下降趋势 (晁云飞等, 2009; Li *et al.*, 2017c), 但是雌蜂会根据寄生时的寄主幼虫状态调整其产卵时子代性别的分配策略 (Li *et al.*, 2019)。当菜蛾盘绒茧蜂起始寄生 3 龄小菜蛾幼虫时, 具有最高繁殖力的子代雌蜂不是育自个体最大的寄主幼虫 (Shi *et al.*, 2002)。颈双缘姬蜂偏好产卵于处在发育早期阶段的小菜蛾蛹, 子代幼蜂的存活率、大小和寄生能力随着寄生时寄主蛹龄的增加而显著降低 (汪信庚等, 1997; Wang and Liu, 2002)。中红侧沟茧蜂虽然能寄生各个龄期的棉铃虫 *Helicoverpa armigera* (Hübner) 和粘虫 *Mythimna separata* (Walker) 的幼虫, 但初始寄生寄主龄期为 1-2 龄幼虫体内发育的子代蜂茧轻于初始寄生寄主龄期为 3-4 龄的, 同时子代幼蜂成功发育的概率随着寄主幼虫龄期增大而下降, 所以母蜂最终表

现为偏好寄生于 2-3 龄的寄主幼虫 (李建成等, 2005; 邴卫弟等, 2006)。斑痣悬茧蜂对其寄主棉铃虫、甜菜夜蛾 *Spodoptera exigua* (Hübner) 幼虫寄生选择可能不是根据寄主龄期而是根据寄主体型大小来评价, 寄生时寄主大小 (发育龄期) 与寄生蜂子代的大小之间呈现“圆顶型”关系, 在个体较大的寄主体内产的寄生蜂卵成功完成发育的概率较低, 同时从卵到成虫的发育时间也会明显延长 (刘亚慧和李保平, 2006; Liu and Li, 2006, 2008; 陈雯等, 2011)。

抑性寄生蜂 (Idiobiont parasitoid) 产卵选择则完全符合“寄主大小-质量假说”, 正如“棉铃虫-棉铃虫齿唇姬蜂 *Campaletis chlorideae* Uchida” (王琛柱, 2001)、“白蜡窄吉丁 *Agrilus planipennis* Fairmaire-白蜡吉丁柄腹茧蜂 *Spathius agrili* Yang” (Wang *et al.*, 2008b)、“菜粉蝶 *Pieris rapae* (Linnaeus)-蝶蛹金小蜂 *Pteromalus puparum* (L.)、广大腿小蜂” (张晓岚等, 2009; 高珏晓等, 2010; 夏诗洋等, 2012)、“哈氏肿腿蜂 *Sclerodermus harmandi* (Buysson)-松褐天牛 *Monochamus alternatus* Hope” (Liu *et al.*, 2011)、“管氏肿腿蜂-青杨天牛 *Saperda populnea* L.” 等寄生系统。周冰颖等 (2016) 的研究表明, 子代成蜂的大小随母代雌蜂初始寄生时寄主个体的大小增加呈线性增加, 母代雌蜂寄生时也会排除个体过小的寄主 (Liu *et al.*, 2011; 周冰颖等, 2016)。在寄生过程中, 寄生蜂雌蜂经常会权衡“trade-off” 出最适合的寄主去产卵, 这是因为寄主的个体大小会对寄生蜂寄生用时以及后代发育的多种适应性指数产生影响 (Li and Sun, 2011; Liu *et al.*, 2011; Wei *et al.*, 2014)。但是有一些容性寄生蜂对寄主幼虫的产卵选择也符合这一假说, 如中红侧沟茧蜂 (刘小侠等, 2004)、蚜茧蜂 *Aphidius transcaasicus* Telenga、可疑柄瘤蚜茧蜂 *Lysiphlebus ambiguus* Haliday 等 (Li and Mills, 2004; Xu *et al.*, 2008)。

卵寄生蜂的发育完全依赖于寄主卵的营养物质, 除了寄主卵的质量 (包括大小、卵龄和种类) 会显著影响寄生蜂母蜂的产卵偏好性, 寄主卵受精与否也是也是影响因素之一。稻螟赤眼蜂 *T. japonicum* (Ashmead)、松毛虫赤眼蜂 *T.*

*dendrolimi* Matsumura、螟黄赤眼蜂 *T. chilonis* Ishii 通过区别受精卵和未受精卵, 偏好产卵于二化螟 *Chilo suppressalis* (Walker) 未受精卵 (Yang *et al.*, 2016) 和米蛾 *Corcyra cephalonica* Stainton 受精卵 (Du *et al.*, 2018)。茶翅蜡沟卵蜂 *Trissolcus japonicus* (Ashmead) 在茶翅蜡 *Halyomorpha halys* (Stål) 未受精卵内发育的子代幼蜂发育时间较短、雌性后代比高、繁殖力强 (Zhang *et al.*, 2017b; Yang *et al.*, 2018b)。类似研究和分析还涉及日本柄瘤蚜茧蜂-黑豆蚜 (甘明等, 2003a)、中红侧沟茧蜂-黏虫 (Li *et al.*, 2006)、麦蛾柔茧蜂-印度谷螟 *Plodia interpunctella* (Hübner) (Akinkulore *et al.*, 2009)、海氏桨角蚜小蜂 *Eretmolerus hayati* Zolnerouich *et* Rose-“B 型”烟粉虱 (Yang and Wan, 2011)、蝇蛹金小蜂 *Pachycrepoideus vindemmiae* (Rondani)-橘小实蝇 (Zhao *et al.*, 2013a)、马尼拉侧沟茧蜂 *Microplitis manilae* Ashmead-甜菜夜蛾 (Qiu *et al.*, 2013)、蝇蛹金小蜂-瓜实蝇 *Bactrocera cucurbitae* (Coquillett) (Zhao *et al.*, 2013b)、管侧沟茧蜂 *Microplitis tuberculifer* (Wesmael)-黏虫 (Chu *et al.*, 2014)、椰心叶甲啮小蜂 *Tetrastichus brontispae* Ferrière-水椰八角铁甲 *Octodonta nipae* (Maulik) (Tang *et al.*, 2014) 等寄生体系。

### 2.3 寄主适合度

经过长期协同进化, 寄生蜂和寄主之间的适合程度 (即寄生蜂对寄主的寄生效能) 很高。生命表参数能反映寄主范围较广的寄生蜂和不同寄主之间的配适程度、相应寄生 (控害) 效能和影响种群波动的因素。不同羽化日龄甘蓝夜蛾赤眼蜂 *Trichogramma maidis* Pint. *et* Voeg 分别用地中海粉斑螟 *Ephestia kuehniella* Zeller 卵繁殖一代后, 其子代蜂对 5 种不同寄主卵的实验种群生命表表明地中海粉斑螟卵可以作为培育优良 (寄主适合度和寄生效能高) 子代蜂的寄主 (邱鸿贵等, 1992; 黄寿山等, 1996)。同样用生命表研究发现, 适合用寄主饲养的还有“荔枝平腹小蜂 *Anastatus japonicus* Ashmead 与不同地理种群的柞蚕 *Antheraea pernyi* Guerin-Meneville 卵” (吕欣

等, 2009)。通过对 24 个不同时期放蜂的放蜂区和对照区内松突圆蚧 *Hemiberlesia pitysophila* Takagi 自然种群生命表参数的分析发现, 影响放蜂区松突圆蚧种群数量变动的关键因子是花角蚜小蜂 *Coccobius azumai* Tachikawa 的寄生, 而对照区内则是其他捕食性天敌的捕食 (古德祥和陈永革, 1998)。影响小菜蛾自然春季种群趋势的是菜蛾啮小蜂 (排除作用控制指数 EIPC=8.28) 和菜蛾盘绒茧蜂 (EIPC=4.85), 影响秋季种群则是 4 龄幼虫被捕食性天敌捕食及其它作用死亡 (何余容等, 2000)。由于豆柄瘤蚜茧蜂 *Lysiphlebus fabarum* Marshall 的  $r_m$  和  $R_0$  值均明显大于黑豆蚜, 所以豆柄瘤蚜茧蜂对黑豆蚜有较强的控害潜能 (王秀梅等, 2014)。不同日龄蝇蛹金小蜂 *Spalangia endius* Walker 对在不同土壤类型及深度化蛹的橘小实蝇 *Bactrocera dorsalis* (Hendel) 的寄生率随着寄主化蛹土壤深度的增加而减少 (唐良德等, 2015)。通过类似分析后明确寄生蜂对既定寄主寄生控制方式和控制效能的还有“异角釉小蜂 *Hemiptarsenus varicornis* (Girault) - 三叶斑潜蝇 *Liriomyza trifolii* (Burgess)” (Cheng *et al.*, 2017)。

### 2.4 寄生效率

寄生蜂和专性捕食者一样, 以一种特定的猎物为食/寄主, 寄生率随着寄主密度的增加而增加, 但最终由于寄生蜂对寄主的处理时间而进入平台期 (Holling II 型)。目前已发现的寄生蜂功能反应曲线均符合 Holling II 模型, 如花角蚜小蜂对松突圆蚧雌成蚧 (王竹红等, 2007)、海氏桨角蚜小蜂对 B 型和 Q 型烟粉虱 (邵家斌等, 2010)、松褐天牛肿腿蜂 *Sclerodermus* sp. 对寄主松褐天牛 3 龄幼虫 (张彦龙等, 2012)、烟蚜茧蜂对桃蚜 *Myzus persicae* (Sulzer) (毕章宝和季正端, 1996; Khan *et al.*, 2016a, 2016b)、横带折脉茧蜂 *Cardiochiles philippinensis* Ashmead 对稻纵卷叶螟 *Cnaphalocrocis medinalis* Guenee (Zhang *et al.*, 1996)、甘蓝潜蝇茧蜂 *Opius dimidiatus* (Ashmead) 对美洲斑潜蝇 *Liriomyza sativae* (Blanchard) 幼虫 (吴启松等, 2002)、冈崎姬小蜂对美洲斑潜蝇 (陈艳, 2005)、啊氏

啮小蜂 *Tetrastichus hagenowii* (Ratzeburg) 对美洲大蠊 *Periplaneta americana* Linnaeus 卵 (张李香和吴珍泉, 2005)、椰心叶甲啮小蜂对椰心叶甲 *Brontispa longissima* Gestro (周祥等, 2006)、菜蛾啮小蜂对小菜蛾幼虫 (Chen *et al.*, 2008)、马尼拉陡胸茧蜂 *Snellenius manila* (Ashmead) 对甜菜夜蛾 (孙君帅和黄寿山, 2010)、白蜡吉丁肿腿蜂 *Sclerodermus pupariae* Yang *et Yao* 对栗山天牛 *Massicus raddei* Blessig (王小艺等, 2010)、蝇蛹蛹小蜂对桔小实蝇蛹 (章玉苹等, 2010)、班氏跳小蜂 *Aenasius bambawalei* Hayat 对扶桑绵粉蚧 *Phenacoccus solenopsis* Tinsley (黄俊等, 2012)、哥德恩蚜小蜂对螺旋粉虱 *Aleurodicus dispersus* Russell (陈俊谕等, 2013)、稻虱缨小蜂对白背飞虱 *Sogatella furcifera* (Horvath) 卵和褐飞虱卵 (Ma *et al.*, 2012) 等。

## 2.5 行为学特性

**2.5.1 母代雌蜂的照料行为** 寄生蜂雌蜂对子代的照料行为, 不仅有利于子代寄生蜂的生长发育, 还能通过降低子代寄生蜂幼蜂的感病率来提高子代幼蜂存活率, 这对寄生蜂种群的维持和繁衍来讲具有正面的影响 (黄维亚和李莉, 2017)。雌性管氏肿腿蜂对高龄子代幼蜂具有节律性的抚育和转移行为 (伍绍龙等, 2013); 缺乏母蜂照料的子代幼蜂感染球孢白僵菌 *Beauveria bassiana* 的比例显著增高 (黄维亚和李莉, 2017)。

**2.5.2 母蜂的学习经历** 雌蜂的学习经历能显著提高其对寄主搜索效率。寄生桑虎天牛 *Xylotrechus chinensis* Chevrolat 的管氏肿腿蜂, 有产卵经验的雌蜂从接蜂到产卵所需的时间显著短于无产卵经验的雌蜂 (张卫光等, 2004)。类似寄生蜂还有川硬皮肿腿蜂 (谢正华等, 2006)、荔蝽平腹小蜂 (王建武等, 2003)、棉铃虫齿唇姬蜂 (Zhang *et al.*, 2010a)、松毛虫赤眼蜂 (欧海英等, 2011) 等。寄生蜂的学习行为受寄生蜂自身生理状态的影响。当中红侧沟茧蜂雌蜂同时被给予食物和寄主相关的气味时, 虽然在一般情况下饥饿的雌蜂更喜欢食物的气味、饱腹的雌蜂更喜欢寄主的气味, 但是已有的产卵经历会提高饥饿雌蜂对寄主气味的偏好性 (Luo

*et al.*, 2013a)。对于多寄主型且学习能力强的寄生蜂, 其适应性的学习能够明显提高其对新寄主的寄生作用, 正如白蜡吉丁肿腿蜂对新寄主-栗山天牛的寄生能力在进行适应性学习后显著提高 (Wei *et al.*, 2013; 唐艳龙等, 2015)。

**2.5.3 雄性蜂的争斗行为** 雄性寄生蜂之间会为了获得更高的与雌蜂交配的机会而发生较为激烈的争斗行为, 这种争斗行为激烈程度和种群中雄性个体的密度以及雌蜂存在与否相关。如舞毒蛾卵平腹小蜂的雄性个体之间争斗行为的强度会随着雄性竞争者的密度和雌蜂的出现而增加, 同时在争斗过程中受伤雄蜂和未受伤的雄蜂相比, 前者更容易受到攻击 (Liu *et al.*, 2017b); 由于增加雄蜂的争斗强度会降低其与雌蜂的交配频率, 雄蜂也会依据雌蜂个体的情况适当调整它们的争斗频率 (Yi *et al.*, 2018)。

**2.5.4 寄生蜂的视觉和嗅觉** 寄生蜂主要是通过触角嗅觉 (气味线索) 接受寄主 (Zhou *et al.*, 2015c), 而视觉在寄生蜂接受寄主的过程中仅起到辅助作用。寄主幼虫的振动和气味线索在白蜡吉丁柄腹茧蜂定位寄主生境和寄主的各个阶段过程中起着重要作用 (Wang *et al.*, 2010), 而寄主蠕动在啮小蜂 *Tetrastichus* sp. 和椰心叶甲啮小蜂雌蜂接受寄主的过程中作用明显 (陆剑锋等, 2005; 周祥等, 2006)。

## 2.6 飞行和扩散

在田间应用寄生蜂的进行生物防治的过程中, 寄生蜂控制害虫的效力在很大程度上取决于它们的移动性, 即是否能迅速到达寄主害虫身边。利用微型昆虫飞行磨计算机联用装置发现不论何种环境条件, 各日龄的雌、雄中红侧沟茧蜂成蜂都能表现出很强的飞行意愿和飞行能力 (Yu *et al.*, 2009)。被寄生的有翅蚜可以携带寄生卵或幼虫进行长途飞行, 由此协助寄生蜂的迁徙和扩散 (Yu *et al.*, 2009; 郭近等, 2010)。虽然寄生后大豆蚜的飞行距离长短对其体内幼蜂的发育时间以及僵蚜率无明显的影响 (Yu *et al.*, 2009), 但是寄生后大豆蚜本身的飞行能力则与寄生发生的时间点和起飞时间之间的间隔长短有关 (Zhang *et al.*, 2012b)。寄生蜂飞行能力和

田间扩散行为与寄生蜂的寄生效率之间具有相关性, 如斑痣悬茧蜂对斜纹夜蛾幼虫 (黄露等, 2011)、花角蚜小蜂对松突圆蚧 (陈顺立等, 2011)、丽蚜小蜂对烟粉虱的寄生率 (赵静等, 2018) 均随释放后飞行和扩散距离的增大而显著降低。

### 3 寄生蜂的生态学

和其他生物一样, 寄生蜂在生态系统也受到生物和非生物因子的影响, 从而影响它们对寄主昆虫的控制效果。

#### 3.1 生物因素

**3.1.1 种间竞争** 在自然界中, 当不同物种利用相似的生态位时, 就会发生竞争性的相互作用。寄生蜂 (寄生蜂) 的寄主范围往往很窄, 需要与竞争对手合作, 利用相同的寄主物种来发育后代。当不同寄生物种的幼虫在同一宿主中发育时, 这就导致了固有的竞争。

不同的寄生蜂携带的寄生因子不同, 能寄生于同一寄主的不同寄生蜂所携带的寄生因子情况决定了寄生蜂的竞争能力。携带不同寄生因子的半闭弯尾姬蜂、菜蛾啮小蜂、菜蛾盘绒茧蜂在寄主体内的种间竞争研究表明这 3 种寄生蜂都不能识别寄主是否已被产卵, 始终处于优势的是菜蛾盘绒茧蜂, 而半闭弯尾姬蜂和菜蛾啮小蜂之间的优势程度由前后产卵顺序和间隔所决定 (施祖华等, 2003; Shi *et al.*, 2004; Bai *et al.*, 2011; Li *et al.*, 2019)。

若是寄生蜂携带的寄生因子种类没有区别, 则寄生蜂本身适应度 (卵孵化较早、寄主选择标准宽松、能识别不同状态的寄主等) 或者抗逆性较强的, 在对寄主的控制上就处于优势地位。如本地寄生蜂拟澳洲赤眼蜂和引进的短管赤眼蜂 *Trichogramma pretiosum* Riley 相比, 单独接蜂时短管赤眼蜂对小菜蛾卵卵龄的要求较为宽松, 对各龄小菜蛾卵的寄生率、子代羽化率、子代雌蜂百分率均较拟澳洲赤眼蜂高, 而子代蜂的发育死亡率则较拟澳洲赤眼蜂低; 当 2 种蜂混接时短管赤眼蜂始终占据优势, 说明短管赤眼蜂对小菜蛾

卵有更强的寄生能力和竞争能力 (何余容等, 2005); 若扩大试验区的面积则发现拟澳洲赤眼蜂可以通过增加搜索区域和寻找更多的寄主来提高它们的竞争能力 (何余容等, 2004)。丽蚜小蜂 *Encarsia formosa* Gahan 和浅黄恩蚜小蜂相比时, 前者对烟粉虱的寄生程度始终要较高 (Pang *et al.*, 2011)。斑痣悬茧蜂和中红侧沟茧蜂相比, 不论是何种不同寄生顺序和间隔时间组合, 前者在黏虫低龄幼虫体内与中红侧沟茧蜂的竞争中占有优势 (徐宇航等, 2016)。花角蚜小蜂和友恩蚜小蜂 *Encarsia amacula* Viggiani *et* Ren 相比, 因其具有种内寄生识别能力而避免过寄生 (袁伟等, 2007)。切割潜蝇茧蜂和长尾潜蝇茧蜂相比, 后者在 30 °C 或者更高的温度条件下对寄主害虫的寄生力明显要高 (杨建全等, 2008)。类似的种间竞争的研究体系还有“枸杞木虱 *Paratrioza sinica* Yang *et* Li-外寄生蜂枸杞木虱啮小蜂 *Tamarixia lyciuni* Yang (膜翅目: 姬小蜂科) 和内寄生蜂枸杞木虱跳小蜂 *Psyllaephagus arenarius* Trjapitzin” (Wu *et al.*, 2018)、“美洲斑潜蝇-豌豆潜蝇姬小蜂和芙新姬小蜂” (Xuan *et al.*, 2018)、“斑翅果蝇 *Drosophila suzukii* Matsumura-反颞茧蜂 *Asobara japonica* Belokobylskij、丽盾瘿蜂 *Ganaspis brasiliensis* Ihering 和细毛瘿蜂 *Leptopilina japonica* Novkovic *et* Kimura” (Wang *et al.*, 2019b)、“绿盲蝽 *Apolygus lucorum* MeyerDurin-红颈常室茧蜂 *Peristenus spretus* Chen *et* van Achterberg 和遗常室茧蜂 *Peristenus relictus* Loan” (Luo *et al.*, 2018)、“东方果蝇 *Bactrocera dorsalis* (Hendel)-阿里山潜蝇茧蜂与切割潜蝇茧蜂” (Yang *et al.*, 2018a)、“橘小实蝇-布氏潜蝇茧蜂 *Fopius vandenboschi* (Fullaway) 和长尾全裂茧蜂” (吕增印等, 2008)。以重寄生蜂之间同样也会发生竞争, 如聚寄生的弯沟啮小蜂 *Baryscapus galactopus* (Ratzeburg) 和单寄生的双菱室姬蜂 *Mesochorus gemellus* Holmgren 相比, 前者更具竞争优势 (Zhu *et al.*, 2016)。

但是, 若同时释放的 2 种寄生蜂之中有一种可以识别和回避已经被寄生的寄主, 那么两者之

间不存在竞争效应,如新引进的抑性外寄生蜂加琳娜柄腹茧蜂 *Spathius galinae* Belokobylskij et Strazenac 雌蜂能识别健康的寄主白蜡窄吉丁虫幼虫和被白蜡吉丁啮小蜂寄生了的寄主幼虫,所以如果 2 种寄生蜂联合释放则两种寄生蜂对寄主的相互竞争作用可能极小(Yang et al., 2012)。

**3.1.2 植物次生代谢物质与挥发物** 植食性昆虫对植物的取食行为会改变植物的次生代谢过程,因此植物的挥发性物质的组成和比例也会发生变化,而这一变化则对寄生蜂搜索起到了正向的引导作用。同时,正在取食或为害的寄主幼虫释放出来的可挥发物对寄生蜂的搜索也起到了正向的引导作用,这在“甘蓝-小菜蛾-半闭弯尾姬蜂”(李欣和刘树生, 2002)、“Bt 棉-非 Bt 棉-甜菜夜蛾-管侧沟茧蜂”(Zhang et al., 2010b)、“水稻-褐飞虱-稻虱缨小蜂”(Lou et al., 2005)、“蓖麻-绿盲蝽-红颈常室茧蜂”(Xiu et al., 2019)的三营养级系统的研究过程中都得到了验证。进一步对寄生蜂搜索能起正向引导作用的挥发物进行了鉴定,发现在“蓖麻-绿盲蝽-红颈常室茧蜂”系统中为间甲苯和 4'-乙基苯乙酮(Xiu et al., 2019)、在“水稻-褐飞虱-稻虱缨小蜂”体系中则是乙烯(Lu et al., 2006)、在“玉米-黏虫-棉铃虫齿唇姬蜂”系统中则是(Z)-3-己烯基乙酸和芳樟醇(Yan and Wang, 2006)。

与昆虫取食一样,喷施某些外源化合物也可诱导植物发生防御反应组成的改变,进而影响了寄生蜂的行为反应(尹姣等, 2005)。如施用外源茉莉酸 JA 可诱导植物产生各种防御反应,在对害虫产生负影响的基础上,提高寄生蜂的搜索和寄生效率(吕要斌和刘树生, 2004; 尹姣等, 2005; 冯会藏等, 2009; Meng et al., 2011; Qiu et al., 2012; Li et al., 2013, 2014b)。当然,具体被喷施的植物器官不同则对寄生蜂的影响不同,芽施 JA 比根施 JA 更能促进寄生蜂的寄生率和搜索频率(Qiu et al., 2012; Li et al., 2013)。能与茉莉酸一样对寄主蜂起诱集作用的挥发类外源施用物还包括茉莉酸甲酯(MeJA)(Cheng et al., 2007; 黄娟娟等, 2015)、水杨酸甲酯(MeSA)(苗进和韩宝瑜, 2011)、果胶

酶(郭光喜等, 2006)、 $\beta$ -葡萄糖苷酶(Wang et al., 2008a)、2,4-Dichlorophenoxyacetic acid (2,4-D)(Xin et al., 2012)、 $\beta$ -1,3-葡聚糖海带多糖(Xin et al., 2019)等。

在作物-害虫-天敌三营养级系统中,过量施用氮素一类的肥料能改变作物的营养成分和次生代谢物质的含量从而对天敌的控害能力产生负面影响(吕仲贤等, 2006)。正如田间氮肥的过量输入对谷类作物上蚜虫的好处大于寄生蜂(Hao et al., 2015)。

**3.1.3 微生物** 在自然界中,寄生蜂和寄主组成的系统会与多种微生物接触,这些微生物有致病性的,也有非致病性,所产生的影响有正面的也有负面的。如斜纹夜蛾核多角体病毒 *Spodoptera litura* multicapsid nucleopolyhedrovirus (SpltMNPV) 就抑制干扰了双斑侧沟茧蜂病毒寄主细胞免疫功能(Luo and Pang, 2006b)。甜菜夜蛾核型多角体病毒-甜菜夜蛾-双斑侧沟茧蜂、核型多角体病毒(NVP)-斜纹夜蛾-淡足侧沟茧蜂的研究表明寄生蜂是可以区别选择健康的、而非被昆虫病毒感染的寄主产卵,若寄生蜂已产卵于被昆虫病毒侵染的寄主,则昆虫病毒就借助寄生蜂产卵管进行传播,所以两者在控制寄主的过程中存在协同性(Jiang et al., 2011, 2014; Cai et al., 2012)。感染烟粉虱的玫烟色拟青霉 *Isaria fumosoroseus*、蜡蚧轮枝菌 *Lecanicillium muscarium* 等昆虫病原真菌对寄生于烟粉虱的桉角蚜小蜂 *Eretmocerus* sp. nr. *furuhashii* 产生了负面性间接影响,即病原菌浓度与寄主体内幼蜂的死亡率呈正相关,但这一间接影响只发生在寄生蜂幼蜂发育的当代(Lazreg et al., 2009; Huang et al., 2010b)。蚜虫体内所携带内共生菌与子代幼蜂的发育关系是内共生菌存在即寄主龄期与幼蜂发育相关。若去除内共生菌则明显降低寄主体内营养物质含量,从而间接影响寄生蜂子蜂的发育(Miao et al., 2004; Cheng et al., 2010)。又如番茄黄化曲叶病毒(TYLCV)通过影响丽蚜小蜂对其传播媒介烟粉虱(B型、Q型)的适合度来影响发育的成蜂寿命(Liu et al., 2014b)。

内共生菌 *Wolbachia* 可以影响寄主蜂的生殖

行为(刘宏岳等, 2009)。田间 *Wolbachia* 在害虫和相应寄生蜂种群之间进行水平相互传播, 正如稻田中灰飞虱 *Laodelphax striatellus* Fallén、褐飞虱、白背飞虱由于被同一种寄生蜂寄生而同时感染同一种 *Wolbachia* (甘波谊等, 2000)。不同生物型烟粉虱所携带的 *Wolbachia* 和它们相应寄生蜂所携带的 *Wolbachia* 在 DNA 序列上的高度相似性支持了 *Wolbachia* 能在害虫和寄生蜂之间进行水平相互传播 (Ahmed *et al.*, 2010)。利用抗生素和高温处理可以降低母蜂感染 *Wolbachia* 的频率 (Wang *et al.*, 2016a, 2016b), 从而影响子代寄生蜂的性比。特别是对于丽蚜小蜂而言, 持续短期高温冲击对母代雌蜂能产生积累效应并降低子代丽蚜小蜂的雌雄性比 (周淑香等, 2009)。虽然使用被 *Wolbachia* 感染的寄生蜂被认为是一种提高生物防治效果的方法, 但在对松毛虫赤眼蜂产雌孤雌品系和两性生殖品系的比较中发现, *Wolbachia* 会对赤眼蜂的适应性产生负面影响 (刘泉泉等, 2018; Liu *et al.*, 2018)。

**3.1.4 中性昆虫** 刺吸式口器的害虫对于蚂蚁来讲是蜜源昆虫, 蚂蚁对蜜源昆虫的照料行为降低了寄生蜂对寄主的控制效能 (程寿杰等, 2013)。如红火蚁 *Solenopsis invicta* Buren 或黑头荒蚁 *Tapinoma melanocephalum* Fabricius 对扶桑绵粉蚧的照料行为不仅能显著降低班氏跳小蜂的寄生率和种群数量, 还能抑制与粉蚧处于竞争性关系的美棘蓟马 *Echinothrips americanus* Morgan 的种群数量, 从而显著促进了粉蚧种群的扩增和繁殖 (程寿杰等, 2013; Zhou *et al.*, 2015a, 2015b)。

**3.1.5 转 Bt 基因抗虫作物** 随着转基因抗虫作物的研发和应用, 抗虫转基因作物对非靶标生物 (寄生蜂) 的潜在影响也是其在商业化种植之前必须进行评估内容。评估结果均表明转基因杀虫植物对寄生蜂的负面影响是经由寄主的品质降低介导, 最终影响寄生蜂种群, 正如直接取食 Cry1Ac 蛋白对寄生蜂无明显影响, 而在取食转 Cry1Ac 基因植物的寄主体内寄生蜂幼蜂的各项发育指标都受到了显著的影响 (Liu *et al.*, 2005a)。相关的研究体系有“转 Cry1Ac 基因棉花-棉铃虫-中红侧沟茧蜂” (任璐等, 2004; Liu

*et al.*, 2005b; Ding *et al.*, 2009)、“表达 Cry1Ac 蛋白的 Bt 玉米-亚洲玉米螟-腰带长体茧蜂” (Wang *et al.*, 2017)。若寄主不受转基因杀虫植物的影响, 其体内发育的寄生蜂则不受影响。正如, “转 Bt 基因水稻-褐飞虱-稻虱缨小蜂/黑肩绿盲蝽”、“转 Bt 基因水稻-谷蠹 *Rhyzopertha dominica* Fabricius、玉米象 *Sitophilus zeamais* Motschulsky - 谷象金小蜂 *Anisopteromalus calandrae* (Howard) - 雅脊金小蜂”体系中的寄主体内能检测到 Bt Cry1Ac 蛋白, 但在寄生蜂幼蜂中都检测不到。所以只要寄主昆虫不是转 Bt 基因作物的靶标害虫, 其体内发育的寄生蜂各项指标均正常 (刘志诚等, 2003; 姜永厚等, 2005; Wei *et al.*, 2008; Han *et al.*, 2014; 梁玉勇等, 2014; 王文晶等, 2014; Chen *et al.*, 2015; Liu *et al.*, 2015; Sun *et al.*, 2015; Tang *et al.*, 2019)。而转 Bt 基因作物的花粉和花蜜、刺吸式害虫产生的蜜露则可以作为寄生蜂成蜂存活的很好补充营养物质 (耿金虎等, 2005; Geng *et al.*, 2006; 白树雄等, 2011; Tian *et al.*, 2018)。

## 3.2 非生物因素

**3.2.1 温湿度** 温度不仅影响到寄生蜂的发育、繁殖和抗逆性, 还对寄生蜂的行为和活动也有显著的影响。不同温度条件下寄生蜂的发育速率不同, 一般情况是温度上升发育速率加快, 但是成蜂的寿命会随着温度的上升而逐渐缩短。寄生蜂只有在最适宜的温度条件下才能发挥最大的寄生能力。在实验室恒温条件下, 发现副珠蜡蚧阔柄跳小蜂 *Metaphycus parasaissetiae* Zhang *et* Huang 世代发育起点温度和有效积温分别为 13.10 °C 和 215.00 度·日, 雌蜂在 27-30 °C 的最适条件下具有最大产卵量, 可达 25.77 粒/雌蜂 (温丽娜等, 2010); 烟蚜茧蜂 *Aphidius gifuensis* (Ashmead) 发育起点温度为 3.3 °C, 有效积温为 2 660 度·日, 雌蜂的寿命、性比、生殖力及僵蚜的体重和羽化率均在 20 °C 时达到最大值, 温度高于 25 °C 时即对烟蚜茧蜂雌蜂各项生物学指标以及寄生习性指标造成显著的负影响 (吴兴富等, 2000); 莫氏蚜茧蜂 *Lysiphlebia mirzai*

Shuja-Uddin 的发育起点温度和有效积温分别为 3.7 °C 和 142.7 度·日, 理论幼蜂、蛹和整个幼期阶段的最适宜发育温度分别是 30.3、33.3 和 31.1 °C, 整个寄生蜂种群增长的最适合温度常在 15-25 °C 之间波动 (Liu and Tsai, 2002)。类似的研究还有颈双缘姬蜂 (汪信庚和刘树生, 1998; Liu *et al.*, 2001)、花角蚜小蜂 *Coccobius azumai* Tachikawa (丁德诚等, 1995)、中华长尾小蜂 *Torymus sinensis* Kamijo (Piao and Moriya, 1992)、菜蛾啮小蜂 (Wang *et al.*, 1999)、白蜡虫啮小蜂 *Tetrastichus kodaikanalensis* Saraswat (焦懿和赵苹, 2000)、冈崎姬小蜂 *Neochrysocharis okazakii* Kamijo (陈艳和叶强, 2002)、底比斯釉姬小蜂 *Chrysocharis pentheus* Walker (詹根祥等, 2002)、玉米螟赤眼蜂 *T. ostrinae* Pang *et al.* (Saljoqi and He, 2004; 代晓彦等, 2016)、卷蛾分索赤眼蜂 *T. bactrae* Nagaraja (陈科伟等, 2005)、桨角蚜小蜂 *Eretmocerus* sp. nr. *furuhashii* (Qiu *et al.*, 2007)、歌德恩蚜小蜂 *Encarsia guadeloupae* Viggiani (Chen *et al.*, 2015)、切割潜蝇茧蜂 *Opius incisus* Silvestri (梁光红等, 2007b)、雅脊金小蜂 *Theocolax elegans* Westwood (高燕等, 2006)、椰甲截脉姬小蜂 *Asecodes hispinarum* Bouek (唐超等, 2007)、白蜡吉丁柄腹茧蜂 (田军等, 2009)、马尼拉侧沟茧蜂 (Qiu *et al.*, 2012)、大蛾卵跳小蜂 (王建军等, 2012)、斑痣悬茧蜂 (Liu *et al.*, 2013)、红颈常室茧蜂 (Luo *et al.*, 2015)、绿眼赛茧蜂 *Zele chlorophthalmus* (Spinola) (李倩等, 2017)、白蜡吉丁啮小蜂 (Duan *et al.*, 2018)、亮腹釉小蜂 *Tamarixia radiata* Waterston (Li *et al.*, 2018)、褐带卷蛾茧蜂 *Bracon adoxophyesi* Mimanikawa (林玉英等, 2018)、丽蝇蛹集金小蜂 *Nasonia vitripennis* Walker (Zhang *et al.*, 2019c) 等。田间调查发现稻虱缨小蜂 *Anagrus nilaparvatae* Pang *et al.* 和拟稻虱缨小蜂 *A. paranilaparvatae* Pang *et al.* 的种群增长的理论最适温度分别为 27.41 °C 和 31.87 °C, 所以稻虱缨小蜂较拟稻虱缨小蜂相比耐高温能力较弱, 不适合在夏季 30 °C 以上条件下释放防治飞虱类害虫 (程遐年

和徐国民, 1991)。

寄生蜂种群内部的遗传变异会造成不同地理种群之间对发育温度要求会有所不同。来自于辽宁朝阳等 5 个地区的松毛虫赤眼蜂不同种群虽然在平均单雌寄生卵量、后代数、后代雌雄比等方面不存在显著差异, 但在 30 °C 条件下, 河北丰宁种群的有效产卵量最高、净生殖力 ( $R_0$ ) 及内禀增长率 ( $r_m$ ) 分别在 129.0-192.1 和 0.269 7-0.446 6 之间波动, 周限增长率 ( $\lambda$ ) 和平均世代历期分别在 1.309-1.545 d 和 11.2-18.99 d 范围内波动 (李莹等, 2013)。

寄生蜂与温度相关的抗逆性可以通过热激蛋白种类、基因的表达水平来体现。蝶蛹金小蜂有分属于 5 个热激蛋白 (HSP) 家族 6 种热激蛋白, 高温和低温诱导、饥饿短期处理、低浓度的重金属离子 ( $Cd^{2+}$ 、 $Cu^{2+}$ ) 的短期胁迫处理后 HSPs 表达水平的升高说明它们在寄生蜂的抗逆过程中能发挥了作用 (Wang *et al.*, 2012)。菜蛾盘绒茧蜂的多个种热激蛋白基因的转录不仅受到高温和低温的诱导, 而且在幼蜂的不同发育阶段转录水平不同, 但是它们的最低转录丰度均出现在 27 °C, 说明了 27 °C 是幼蜂发育的最适宜温度 (Shi *et al.*, 2013b)。同样, 美国白蛾 *Hyphantria cunea* (Drury) 的优势内寄生蜂白蛾周氏啮小蜂 *Chouioia cunea* Yang 的 5 个 HSP 基因表达丰度会因温度 (高温或低温) 处理、农药处理和紫外线辐射处理显著的上升 (Pan *et al.*, 2018)。螟黄赤眼蜂的 6 个 HSP 基因表达丰度在 32 °C 和 40 °C 处理 1 h 全部能显著上升, 但在相对低温 10 °C 和 17 °C 的处理 (时长为 1 h) 却没有任何相应, 说明螟黄赤眼蜂对冷、热处理的敏感度不同 (Yi *et al.*, 2018)。

全球变化的主要驱动因素之一是气温升高, 作物、植食性害虫和它们的天敌 (寄生蜂) 之间的三营养层之间互作过程中发挥重要作用。用红外加热装置在我国北方常规和免耕麦田模拟气候变暖, 发现作物的生物量以及物候从返绿期到成熟期延长了 6-11 d, 若寄生蜂的种群动态和寄主麦长管蚜错开, 则寄主麦长管蚜的数量会显著增加, 即寄生蜂的控制效果下降, 但若 2 种种群动态相一致, 则寄生蜂的寄生率会显著增加

(Dong *et al.*, 2013), 所以寄生蜂对气候变暖的反应是与自身种群波动与寄主种群波动的配适度相关。35 °C 温度冲击松毛虫赤眼蜂处于发育中、后期的蛹仅 6 h 就可降低羽化出蜂率、单卵出蜂数, 而 40 °C 的单次冲击 6 h 则幼蜂不能继续发育(耿金虎等, 2005)。用人工模拟高温暴露处理发现对花角蚜小蜂雌成虫造成热伤害的高温累积下限(LLSEHIT)随着季节性平均气温、极端高温的升高表现出明显的升高趋势, 所以花角蚜小蜂季节耐热性大小次序为夏季>秋季>春季(钟景辉, 2010)。类似高温胁迫研究的对象体系还有卷蛾分索赤眼蜂-鳞翅目害虫(Wang *et al.*, 2014)、短翅蚜小蜂 *Aphelinus asychis* Walker-桃蚜(Wang *et al.*, 2016a)、斑痣悬茧蜂-斜纹夜蛾(孟倩等, 2017)、白翅金小蜂 *Pteromalus albipennis* Walker (Pteromalidae)-股花翅实蝇 *Tephritis femoralis* Chen (Xi *et al.*, 2017)、沃氏桨角蚜小蜂 *Eretmocerus warrae* Naumann *et* Schmidt 或丽蚜小蜂-温室白粉虱(Wang *et al.*, 2019a)、海氏桨角蚜小蜂和浅黄恩蚜小蜂-烟粉虱(段敏等, 2016; Zhang *et al.*, 2019b)、可疑柄瘤蚜茧蜂-黑豆蚜(徐清华等, 2007)、淡足侧沟茧蜂-甜菜夜蛾(Jiang *et al.*, 2018)。

除了温度这一气候变化因素外, 湿度(干旱与否)也对生态系统中的各级营养系统有较强的影响。如随着水分亏缺水平的增加, 麦长管蚜 *Sitobion avenae* (Fabricius) 无性系的发育速度趋于缓慢、烟蚜茧蜂对麦长管蚜的寄生率也逐渐下降, 说明干旱对寄生蜂具有负面影响(Ahmed *et al.*, 2017)。

**3.2.2 光照和颜色** 光被认为是影响昆虫生物学、生理学和行为特征的关键环境线索。不同的寄生蜂对不同波长和强度的趋性不同, 如低光强的蓝光和绿光引起管氏肿腿蜂的正向趋光性反应(Luo and Chen, 2016)。丽蚜小蜂对短波长的光比长波的光更敏感, 低强度紫光或紫外光就能引发其趋光性反应(Chen *et al.*, 2016b); 长日照光周期和高光强度还能促进白蜡吉丁肿腿蜂产生更多的雌性子代(Hu *et al.*, 2019)。所以

通过调控光照条件提高寄生蜂田间释放和控害的效率。

颜色和光线一样, 也是影响寄生蜂行为的环境因素之一, 即不同的寄生蜂对颜色也表现出的不同的趋性。对六盘山、大兴沟和新宾地区研究姬蜂成蜂对颜色的反应发现, 黄色和绿色捕集器比其他颜色能诱集更多的姬蜂, 不同地区姬蜂对颜色的喜欢存在差异(Li *et al.*, 2012); 螟黄赤眼蜂趋向于选择亮度高(白色和粉红色)的颜色(汪庚伟等, 2015)。所以筛选合适的蜜源植物(花的颜色)也能有效诱集寄生蜂, 从而提高寄生蜂释放后控害的效果。

**3.2.3 化学农药** 在自然界中, 寄生蜂和寄主相互依存, 使用杀虫剂会对两者同时产生影响。天敌对农药的敏感性是生物防治过程中天敌与化学农药协调使用的科学依据。通常, 施用过高剂量的杀虫剂会在防治寄主的同时杀死寄生蜂, 即在寄主体内发育的幼蜂和自由生活的成蜂, 由此使用杀虫剂后害虫种群数量反弹较快(Yang *et al.*, 2015; Zhu *et al.*, 2018a)正如“茚虫威 Indoxacarb 和多杀菌素 Spinosad 对短管赤眼蜂”(Liu and Zhang, 2012)、“三唑磷、溴氰菊酯、氯虫酰胺和吡蚜酮对稻虱缨小蜂”(Liu *et al.*, 2012)的致死作用。三氟唑啉啉与其它杀虫剂相比对稻虱缨小蜂、黑肩绿盲蝽和赤眼蜂等褐飞虱天敌则无影响(Zhu *et al.*, 2018b)。

寄主与寄生蜂在抗药性的产生和发展上存在协同性, 即寄主的抗药性既能减少杀虫剂对体内发育着的幼蜂的影响, 还能培育出具有类似耐药性的后代寄生蜂。如用抗性小菜蛾幼虫连续多代饲养和培育寄生蜂, 则可以筛选出具有抗性的寄生蜂(李元喜等, 2002a, 2002b; Liu *et al.*, 2003, 2004, 2007); 存在于萝卜蚜 *Lipaphis erysimi* (Kaltenbach) 体内的甲胺磷能诱导在萝卜蚜体内发育的菜蚜茧蜂 *Diaerettilla rapae* (Mcintosh) 幼蜂对甲胺磷产生抗性(Wu *et al.*, 2009)。由于寄主的发育历期会因使用了亚致死剂量的杀虫剂而延长, 即寄主最适被寄生期延长, 所以寄生蜂寄生率上升(Cai *et al.*, 2009; Qian *et al.*, 2012), 因此施用亚致死剂量的杀虫

剂对于寄生和寄生蜂体系产生了正影响。

**3.2.4 其他因素** 环境中的重金属污染、CO<sub>2</sub> 浓度也会对寄生蜂寄生能力产生影响。如寄主棕尾别麻蝇体内的营养水平由于 Cu<sup>2+</sup> 胁迫而下降, 在其体内发育的丽蝇蛹集金小蜂子蜂就受到了负面影响, 表现在生长和发育延缓、繁殖力(卵黄原蛋白的合成)的下降(Ye *et al.*, 2009), 但是耐 Cu<sup>2+</sup> 棕尾别麻蝇品系培育出来的丽蝇蛹集金小蜂在 Cu<sup>2+</sup> 的胁迫下有较高的寄生率和后代产出量(董卉等, 2008)。同样, 连续取食添加 Zn<sup>2+</sup> 饲料的斜纹夜蛾幼虫对其体内的双斑侧沟茧蜂的生存与发育也会产生负影响, 即随着斜纹夜蛾幼虫血淋巴中 Zn<sup>2+</sup> 浓度的增加, 双斑侧沟茧蜂的寄生率和子代蜂羽化率降低(夏婧等, 2006)。寄主昆虫对寄生蜂的防御能力会因为环境中 CO<sub>2</sub> 浓度或食物质量的变化而变化, 具体为随着 CO<sub>2</sub> 浓度的升高和食物质量变好, 寄主昆虫的防御能力增强(Yin *et al.*, 2014)。

## 4 寄生蜂对寄主生理、发育、生殖、行为的调控

### 4.1 寄生因子及功能

寄生蜂携带的寄生因子是成功寄生的关键因素, 这些因子有在主动防御中发挥抑制作用毒液、多 DNA 病毒(Polydnavirus, PDV)、畸形细胞和在被动逃避中发挥作用的卵巢蛋白、幼蜂胚胎分泌物等。

**4.1.1 毒液** 毒液是所有寄生蜂携带的寄生因子, 是由寄生蜂毒腺分泌并储存在毒囊中、在寄生时注射到寄主体内的蛋白混合物。根据寄生蜂的寄生习性, 不同寄生蜂毒液对寄主的作用可以分成抑性寄生蜂的毒液和容性寄生蜂的毒液; 根据寄生蜂是否还具有不同的寄生因子则可以分单毒液作用和毒液与其它因子的复合作用。

寄生蜂体内产生和分泌毒液的器官具有相对稳定的特征, 正如对菜蛾盘绒茧蜂和半闭弯尾姬蜂(潘健和陈学新, 2003)、黄腹潜蝇茧蜂(万志伟等, 2005; Wan *et al.*, 2006)、腰带长体茧蜂(陆剑锋等, 2006)、蝶蛹金小蜂(Zhu *et al.*,

2008c)和管氏肿腿蜂(朱家颖等, 2011)的毒液器官超微机构观察发现:(1)毒腺形态有单条的、二叉的和多分枝的, 分泌细胞层、退化的外胚层细胞和环腔的内膜层这 3 层细胞构成了细胞层, 其中分泌细胞层细胞内有发达的内质网、分泌囊泡、分泌颗粒、液泡、末端附器等细胞器;(2)毒囊可分成外鞘肌肉层、中间层和细胞核较大的上皮细胞层;(3)毒腺中还存在类病毒颗粒(Virus-like particle, VLP)和小 RNA 病毒。

寄生蜂毒液的主要成份是蛋白及多肽。聚丙烯酰胺凝胶电泳(SDS-PAGE)分析表明, 黄腹潜蝇茧蜂(万志伟等, 2005)、颈双缘姬蜂(郇卫弟等, 2006)、菜蛾盘绒茧蜂(Yu *et al.*, 2007)和腰带长体茧蜂(李永等, 2007)等寄生蜂毒液蛋白的分子量大多都在 100 kD 以下。而进一步质谱鉴定表明, 其中除了钙调蛋白、丝氨酸蛋白酶、精氨酸激酶等多种蛋白质和酶外(Zhu *et al.*, 2010a), 还存在抑菌物质, 如蝶蛹金小蜂毒液中的抗菌肽 PP13、PP102 和 PP113(Shen *et al.*, 2010)、丽蝇蛹集金小蜂和菜蛾盘绒茧蜂毒液中的 defensin 类抗菌肽(Tian *et al.*, 2010; Ye *et al.*, 2010; Wang *et al.*, 2013b)和川硬皮肿腿蜂毒液中对金黄色葡萄球菌 *Staphylococcus aureus* 生长具有抑制作用的短肽(卓志航等, 2013a)。

寄生蜂毒液在寄生蜂产卵时注入寄主体内并发挥对寄主免疫和行为的调控作用。就抑性寄生蜂而言, 寄生蜂毒液可以使寄主的免疫完全受到抑制并停止发育(神经毒性), 而容性寄生蜂的毒液虽然也能部分抑制寄主的免疫, 但是鲜有神经毒性, 所以对寄主的发育几乎没有影响(严智超等, 2017)。如管氏肿腿蜂对寄主双条杉天牛幼虫的蜇刺或者寄生(注射毒液)可以导致寄主完全麻痹并在长时间内保持新鲜的柔软、不变质、不腐烂状态(张卫光等, 2004), 而川硬皮肿腿蜂毒液对寄主黄粉甲的麻痹作用是可逆的、具剂量效应的(卓志航等, 2013b)。

对于只携带毒液的寄生蜂而言, 毒液在调控寄主的过程中发挥了关键作用。毒液既能影响寄主的细胞免疫反应, 包括降低寄主血细胞数量, 抑制血细胞粘附及包裹能力等, 又能抑制寄主的

体液免疫, 包括血淋巴黑化反应等。如黄腹潜蝇茧蜂毒液抑制寄主血细胞的包囊作用 (Wan *et al.*, 2005) 以及蝶蛹金小蜂毒液显著减少寄主菜粉蝶蛹血细胞总数、抑制其血细胞延展、降低其包囊和吞噬能力和黑化能力 (Cai *et al.*, 2004; 张忠等, 2004; Tian *et al.*, 2010; Fang *et al.*, 2011a; 张倩倩等, 2011; Zhang *et al.*, 2012a)。同样抑制作用的出现在寄主为亚洲玉米螟的蛹啮小蜂 *Tetrastichus* sp. 毒液 (任丹青等, 2004) 和腰带长体茧蜂毒液 (冯从经等, 2004; Li *et al.*, 2007)、寄主为黄粉虫的川硬皮肿腿蜂毒液 (卓志航等, 2013b)、寄主杨小舟蛾蛹的白蛾黑基啮小蜂毒液 (于艳华等, 2015)、寄主为美国白蛾蛹的白蛾周氏啮小蜂毒液 (辛蓓等, 2016)。而这种细胞免疫抑制作用的发挥多为寄生蜂毒液抑制寄主多种免疫调控通路组成基因的表达和直接参与抑制寄主细胞免疫。如蝶蛹金小蜂毒液可抑制寄主菜粉蝶蛹内细胞免疫识别关联基因 (革兰氏阴性菌结合蛋白、肽聚糖识别蛋白、 $\beta$ -1,3-葡聚糖识别蛋白基因、清道夫受体 Scavenger receptor) 的表达 (Fang *et al.*, 2010, 2011b; 朱家颖等, 2010), 进而还会抑制寄主血细胞和脂肪体中 C-type lectin、cecropin、lysozyme、attacin 和 leucocin 等多种免疫效能基因的表达 (Fang *et al.*, 2010, 2011a, 2016); 后者如毒液钙网蛋白 (Wang *et al.*, 2013a)。在独立发挥作用的毒液影响寄主的血淋巴黑化反应的过程中, 毒液蛋白一般是直接与寄主酚氧化酶原激级联反应组分结合形成复合物进而削弱寄主体液免疫水平, 如丽蝇蛹集金小蜂毒液中含有的 Pacifastin 蛋白酶抑制剂 NVPP-1、NVPP-2 及 NvSPPI (钱岑等, 2013; Qian *et al.*, 2017) 和蝶蛹金小蜂毒液 serpin 蛋白的一个活性剪接体与寄主血淋巴中酚氧化酶原激活蛋白能直接形成复合物 (Yan *et al.*, 2016; 严智超等, 2017); 或者引发寄主酚氧化酶原激级联反应中负调控因子的表达上调, 如蝶蛹金小蜂毒液导致寄主菜粉蝶蛹 serpin 基因的表达量显著上调 (Zhu *et al.*, 2015b)。

对于还携带其他因子如 PDVs 的寄生蜂而

言, 毒液往往无明显作用、有作用但只能维持较短的时间或者仅是对其他因子起到辅助增效作用。携带 CvBV 的菜蛾盘绒茧蜂毒液仅在寄生后 4 h 内对寄主小菜蛾浆血细胞延展和活力具有暂时的抑制作用, 但它可协同和强化萆液 (含 CvBV) 对寄主血细胞的作用, 抑制血细胞延展, 导致血细胞降解和死亡 (Yu *et al.*, 2007)。携带 DsIV 的半闭弯尾姬蜂毒液抑制寄主血细胞延展的作用则在处理后 24 h 内, 随后寄主小菜蛾血细胞延展能力和颗粒血细胞吞噬作用都恢复正常 (Huang *et al.*, 2010a; 黄芳等, 2011a)。携带 CgBV 的粉蝶盘绒茧蜂 *Cotesia glomeratus* (Linnaeus) 对寄主菜粉蝶幼虫的血淋巴黑化反应无显著影响 (Zhu *et al.*, 2011b)。二化螟盘绒茧蜂毒液虽不影响寄主二化螟的血细胞免疫功能, 但它可协同萆液降低寄主幼虫血淋巴中血细胞总数、抑制血细胞粘附、包囊和血淋巴黑化能力 (Teng *et al.*, 2016)。

在明确毒液综合作用后, 研究人员开始着手分离毒液中的活性蛋白成分并开展功能研究。滤膜截留法 (不同分子量) 与 75%硫酸铵盐析法的组合是现今已知的、对毒液蛋白活性影响最低、分离速度最快的纯化方法 (吴玛莉等, 2008), 由此获得了能对寄主菜粉蝶血细胞延展和包囊起抑制作用的蝶蛹金小蜂毒液活性蛋白 Vn11, 该蛋白大小为 24.1 ku (Wu *et al.*, 2008) 和川硬皮肿腿蜂毒液中分子量为 51.17 ku 的蛋白能对寄主黄粉虫起麻痹作用 (卓志航等, 2013a)。高通量毒腺转录组测序的介入使菜蛾盘绒茧蜂、颈双缘姬蜂、蝶蛹金小蜂等寄生蜂毒液蛋白的研究得到发展, 在明确酸性磷酸酶等的活性蛋白及酶的基因编码序列后, 对这些基因的转录动态、重组蛋白制备、抗体制备、组织定位等开展研究, 阐明了在寄生蜂寄生寄主后, 它们所发挥的作用 (Zhu *et al.*, 2008b, 2010b, 2011b; Wang *et al.*, 2013a; Yan *et al.*, 2016; Yang *et al.*, 2017c; Zhao *et al.*, 2017)。

**4.1.2 多 DNA 病毒** 多 DNA 病毒 (Polydnavirus, PDV) 是一类与茧蜂科和姬蜂科寄生蜂有专性共生关系的、仅在雌蜂卵巢中复制、具有独特的分

段 DNA 基因组的特殊病毒, 随寄生蜂卵进入寄主体内。在借助电子显微镜技术手段等对中红侧沟茧蜂病毒 (*Microplitis mediator* bracovirus, MmBV) (李馨等, 2001)、菜蛾盘绒茧蜂病毒 (*Cotesia vestalis* bracovirus, CvBV) (白素芬等, 2003) 和棉铃虫齿唇姬蜂病毒 (*Camponotus chloridiae* ichnovirus, CcIV) (Yin *et al.*, 2003) 核衣壳的数量、大小和直径以及采用电泳法检测了基因组的片段化等的基础上, 对棉铃虫齿唇姬蜂病毒 (Tian *et al.*, 2007)、双斑侧沟茧蜂病毒 (*Microplitis bicoloratus* bracovirus, MbBV) (Luo and Pang, 2006a) 和菜蛾盘绒茧蜂病毒 (Chen *et al.*, 2007, 2008; 刘鹏程等, 2008; Shi *et al.*, 2008a, 2008b) 等多 DNA 病毒在寄主体内的转录种类 (Vankyrin、PTP、EP-like、Cys-motif 和 cysteine-rich motif 等)、时空动态进行分析, 还克隆了其中一些基因并对产物进行了分布定位。同时, 通过观察处于各个蛹日龄的半闭弯尾姬蜂卵巢的发育进程后发现其萼区有病毒颗粒的存在, 这些病毒颗粒的特征与典型姬蜂病毒相一致所以命名为半闭弯尾姬蜂病毒 (*Diadegma semiclausum* ichnovirus, DsIV) (Huang *et al.*, 2008b)。为了进一步了解 PDVs, 利用转录组和基因组研究技术研究了 PDVs 编码的基因, 如 CvBV 的全基因组序列的直接测定和注释 (Chen *et al.*, 2011c), 又如通过测定寄生后寄主组织转录组鉴定了部分二化螟盘绒茧蜂病毒 (*Cotesia chilonis* bracovirus, CchBV) (Wu *et al.*, 2013; Qi *et al.*, 2015)、双斑侧沟茧蜂病毒 (Li *et al.*, 2014a) 的基因家族 (编码序列)。

进入寄主体内后, 整合到寄主基因组上的 PDVs 启动相关基因表达并合成产物来影响寄主免疫、发育和代谢过程, 从而保障寄生蜂幼蜂发育。PDVs 对寄主免疫抑制表现为降低血淋巴酚氧化酶 PO 活性 (Yin *et al.*, 2001)、抑制寄主血细胞的延展并由此影响对凝胶珠和寄生蜂卵的包裹作用 (Yin *et al.*, 2003; Zhang and Wang, 2003; Yu *et al.*, 2007)、引起寄主血细胞凋亡 (Luo and Pang, 2006b)、降低寄主酚氧化酶原基因 PPO 的转录丰度 (Zhu *et al.*, 2011b) 来抑制寄主体

液黑化反应 (Zhu *et al.*, 2011b; 刘君等, 2014)。最近研究发现, PDVs 的环状基因组中还编码了多个 miRNA 种子序列, 在整合到寄主基因组后会在组织细胞内持续转录产生活性 miRNAs, 从而在基因转录水平上对寄主的免疫和发育发挥调控作用 (Wang *et al.*, 2018)。

**4.1.3 畸形细胞** 通常, 被称之为畸形细胞的一类细胞是寄生蜂胚胎发育过程中自浆膜层解离并释放到寄主血腔中的巨型细胞。对中红侧沟茧蜂、菜蛾盘绒茧蜂、烟蚜茧蜂畸形细胞的研究发现, 活力旺盛的细胞表面微绒毛丰富、内部细胞器 (高尔基体、内质网) 众多、细胞核分多叉、细胞器和细胞膜附近分泌小泡众多, 能合成大小在 40.98-94.64 kD 的多种蛋白, 而处于寄生后期的畸形细胞胞内细胞器数量减少、出现大量空腔、表面微绒毛联合、变大, 细胞内容物外溢, 最终会因凋亡而分解; 寄生后寄主的取食情况会对体内畸形细胞的数量、活性产生负面影响 (秦启联等, 2000a; 白素芬等, 2002, 2005a, 2008; 白素芬和陈学新, 2009; 刘金文等, 2008, 2011)。菜蛾盘绒茧蜂畸形细胞 TATA 结合蛋白基因是我国克隆的第一个寄生蜂畸形细胞编码基因 (潘璟等, 2014), 随后对菜蛾盘绒茧蜂畸形细胞转录组的测定和分析发现, 畸形细胞既可以通过产生毒液类似蛋白抑制寄主血淋巴的黑化, 也可以合成分泌活性抗菌肽来补充寄主由于寄生被抑制的体液免疫, 以提高被寄生的寄主抵抗病原体感染的能力, 起到了双向免疫调控功能 (Gao *et al.*, 2016)。通过进一步深入分析和比较菜蛾盘绒茧蜂畸形细胞与寄主组织的转录组数据发现了有畸形细胞产生的菜蛾盘绒茧蜂特异性 miRNAs 出现在寄主组织中, 由此通过进一步的体内定量检测比较和体外转运的研究证明了寄生蜂畸形细胞可以产生 miRNAs 并通过外泌体跨膜转运到寄主组织细胞中、在基因转录后水平调控寄主的各项生理过程 (Wang *et al.*, 2018)。

**4.1.4 其他因子** 除了毒液、PDVs 和畸形细胞这些典型的寄生因子之外, 寄生蜂还携带有病毒样纤丝 (VLFs)、小 RNA 病毒等。在中红侧沟茧蜂雌蜂侧输卵管中 (秦启联等, 2001)、黄腹

潜蝇茧蜂毒腺内 (Wan *et al.*, 2006) 存在的类病毒颗粒 (VLPs) 和菜蛾盘绒茧蜂卵表面存在的类病毒纤丝 (VLFs) 和纤丝层能干扰寄主血细胞对蜂卵的识别从而抑制了随后的包裹作用 (白素芬等, 2009)。通过测定存在于蝶蛹金小蜂毒腺的小 RNA、双顺反子病毒 (PpSRV) 的基因组序列并进行注释后发现, 其核糖体进入位点和核衣壳蛋白基因的编码序列分别为 3 个主肽 (28、31、38 ku) 和 1 个小肽 (9.6 ku) (Zhu *et al.*, 2008a), 对其功能研究表明 PpSRV 并不改变寄主的生理, 但能通过减少子代雌性个体对寄生蜂自身种群的性比起调控作用 (Wang *et al.*, 2017)。

## 4.2 寄生蜂对寄主免疫、代谢、发育、生殖、行为的影响

通过长期协同演化, 寄生蜂及其寄主间已经形成了一套稳定的互作体系。寄生蜂为了确保其后代能够在寄主害虫体内顺利完成发育对寄主的生理过程或多或少均产生影响, 这也导致寄主在行为、免疫、营养代谢、内分泌与生长发育等水平上产生显著变化。寄生蜂对寄主的调控作用是寄生蜂应用于生物防治的理论基础, 而寄生蜂对寄主行为、免疫系统、营养代谢、内分泌与生长发育等的调控作用的类型和作用强度决定了其应用于生物防治的潜力。

**4.2.1 对寄主免疫的影响** 昆虫的免疫系统包括细胞免疫和体液免疫。在寄生蜂和寄主相互作用的过程中, 寄主的免疫系统是寄生蜂子代成功发育首先要克服的第一个屏障, 经过两者的长期协同进化, 寄生蜂利用自身携带的寄生因子 (毒液、PDVs 以及畸形细胞等) 在寄生过程中形成了有效克服寄主免疫系统的多种策略。根据应对寄主免疫防御的方式, 寄生蜂可以被称之为主动抑制型和被动逃避型。

### (1) 抑制寄主细胞免疫

寄生蜂对寄主细胞免疫的抑制首先是引起寄主血细胞数目的变化 (变多或减少)、细胞死亡增多以及细胞延展和包裹的抑制。正如二化螟盘绒茧蜂 *Cotesia chilonis* Munakata 寄生后的二化螟幼虫血细胞数量上升 1.53-2.79 倍、包裹能

力下降 (杭三保和陆自强, 1991)、蝶蛹金小蜂寄生导致寄主菜粉蝶、柑橘凤蝶 *Papilio xuthus* Linnaeus 血细胞数降低 (血细胞因细胞器被破坏和减少而死亡), 由此浆血细胞的延展受到抑制 (蔡峻等, 2001, 2002; Cai *et al.*, 2004; 张忠等, 2005; Zhang *et al.*, 2005, 2012a)、颈双缘姬蜂寄生虽能导致寄主小菜蛾蛹血细胞 (浆血细胞和颗粒血细胞) 总数上升, 但浆血细胞和颗粒血细胞会发生破裂和死亡以及浆血细胞的延展受限 (郇卫弟等, 2006)、半闭弯尾姬蜂的寄生降低小菜蛾血细胞总数 (Huang *et al.*, 2009b)、椰心叶甲啮小蜂寄生后的寄主椰心叶甲蛹内血细胞的数目、浆血细胞延展能力表现为先低后高的情况 (刘奎等, 2008)、棉铃虫齿唇姬蜂的寄生明显减少了棉铃虫、粘虫血细胞的数目 (Han *et al.*, 2013; Wang *et al.*, 2015)。寄主血细胞数目由于寄生蜂而变多的机制目前还不清楚, 但是由寄生蜂导致寄主血细胞数量减少的机制, 通过比较两种不同类型寄生蜂 (菜蛾盘绒茧蜂和半闭弯尾姬蜂) 同时寄生小菜蛾的过程发现, 可能存在两种情况: 一是寄生蜂寄生造成寄主成熟血细胞死亡 (Yu *et al.*, 2007), 或是寄生后造血器官的坏死造成新生血细胞的减少 (Huang *et al.*, 2009b)。而寄生蜂寄生导致寄主成熟血细胞死亡的可能原因之一则可能是寄主细胞线粒体膜通透性受到寄生的影响为发生改变, 以及与细胞存活相关连的基因转录发生了变化 (Li *et al.*, 2014a)。属于免疫逃避型的腰带长体茧蜂的寄生不影响亚洲玉米螟和欧洲玉米螟 *Ostrinia nubilalis* (Hubner) 的细胞免疫, 但在蜂卵和胚胎表面分布的纤维层和 Hemomucin 蛋白是帮助蜂卵/胚胎避免被寄主血细胞包裹的主要因素 (Hu *et al.*, 2003, 2014)。

### (2) 抑制寄主体液免疫

昆虫体液免疫最主要是血淋巴的黑化反应 (酚氧化酶激活级联反应) 和抗菌肽两个方面。寄生蜂寄生降低了寄主血淋巴酚氧化酶 PO 活性的研究报道于棉铃虫齿唇姬蜂-棉铃虫/黏虫 (Yin *et al.*, 2001; Han *et al.*, 2013)、颈双缘姬蜂-小菜蛾 (郇卫弟等, 2006; 黄芳等, 2011b)、椰甲

截脉姬小蜂/椰心叶甲啮小蜂-椰心叶甲(刘奎等, 2009; 宋晓君等, 2009)等体系。寄生蜂的寄生还抑制寄主防御素 defensin、天蚕素 cecropin 等抗菌肽基因以及溶菌酶、溶血素抗菌活性蛋白基因的转录(Gao and Zhu, 2010; 王颖颖等, 2015; Fang *et al.*, 2016), 以减少寄主体内总活性抗菌物质产生的形式抑制了寄主的体液免疫, 以至于离体培养寄生后的寄主血淋巴感菌率提高(黄芳等, 2011b)。有趣的是, 从寄生蜂(菜蛾盘绒茧蜂)幼蜂胚胎分离、协同发育的畸形细胞中同时分泌黑化抑制因子以及抗菌肽到寄主血腔内, 在抑制寄主免疫的同时又有针对性的增强抵抗外源病原物的能力, 这样对寄主的免疫就起到了抑制和补充的双向调节作用(Gao *et al.*, 2016)。双斑侧沟茧蜂幼蜂还会分泌超氧化物歧化酶(SOD)来降低寄主体内局部微环境的活性氧水平, 从另一个方面降低了寄主体液免疫防御并保障自身的发育(Zhang *et al.*, 2019a)。

**4.2.2 对寄主营养代谢的影响** 寄生蜂的幼期通过取食寄主血淋巴中的物质获得营养和能量已获得维持生长和发育的必需物质, 那么寄主昆虫的代谢过程也在寄生蜂的影响下向有利于寄生蜂子代获取营养的方向转向, 同时寄主储存在自身脂肪体等组织中的营养物质也会因为寄生蜂的作用释放到血淋巴循环系统中以供发育中的幼蜂获取。

#### (1) 对寄主营养器官的影响

昆虫的营养代谢系统是由多个器官协调运作的复杂系统, 其中消化道和脂肪体是这一系统中参与食物同化、储存和代谢的最重要的两个器官。寄主被寄生蜂寄生后, 其体内的与营养代谢相关的脂肪体的组织受到不同程度的影响, 表现为整体结构松散、细胞内营养物质显著减少, 而脂肪体细胞内则是细胞器结构被破坏并趋于解体、数量锐减、细胞核内染色质异常等状态, 而造成这样情况的原因首先是寄生蜂的畸形细胞能附着在寄主脂肪体表面将脂肪体分解成颗粒状, 其次是多 DNA 病毒和毒液使脂肪体细胞内的脂质体变得小而密集、线粒体和内质网等细胞器变化、糖原积累(白素芬等, 2003, 2005b,

2006; 谭毅和周祖基, 2003; 狄蕊等, 2006; 汪海燕等, 2006; 郦卫弟等, 2007)。而这些变化都是促进寄主营养从脂肪体中释放有利于幼蜂获取有关。寄生蜂寄生所造成寄主中肠颜色由正常发育时的绿色变为黄色并出现红色斑点则反映了寄主消化道功能的异常, 而此时寄主体壁红斑的出现、气管组织颜色变暗(呈棕黑色)乃至无韧性或萎缩、丝腺细胞不发育膨大就发生凋亡以及由于肌肉组织高度解体暴露内骨骼等的出现(谭毅和周祖基, 2003; 万志伟等, 2005; 狄蕊等, 2006; 黄芳等, 2014)则说明这些组织可能由于得不到维持发育或者功能所必需的营养物质而发生了病变或者退化, 进一步表明寄主的营养代谢已经转向到为寄生蜂幼蜂提供营养的方向。

#### (2) 对寄主营养代谢过程的影响

子代寄生蜂发育所需要的营养都是由寄主供给, 寄生会改变寄主体内脂类、糖类、氨基酸以及蛋白质等营养物质的合成、种类、含量和浓度, 寄主细胞内营养物质积累转向被动消耗以满足寄主体内幼蜂发育时营养的需求(白素芬等, 2006)。寄生蜂以及寄生因子借助改变营养物质代谢关联功能酶转录丰度来改变相关酶总含量或总酶活, 如菜蛾盘绒茧蜂寄生就降低了小菜蛾中肠消化酶(胰蛋白酶和类凝乳蛋白酶)基因的转录丰度, 相应的降低了产物酶的活性(Shi *et al.*, 2009, 2013b)、蝶蛹金小蜂通过降低一些如 masquerade-like serine proteinase 在内基因的转录水平显著降低了对应蛋白含量(Zhu *et al.*, 2011a), 从而造成排泄、呼吸、消化和同化作用等营养、代谢过程的改变(Huang *et al.*, 2008a)。

**寄主血淋巴游离氨基酸:** 寄主血淋巴内游离氨基酸总浓度因寄生蜂的寄生而上升, 但具体各种氨基酸浓度变大则因不同的寄生蜂和寄主体系而不同。二化螟盘绒茧蜂寄生导致二化螟幼虫血淋巴中含量变化最大的 4 种氨基酸是苏氨酸、丝氨酸、赖氨酸、精氨酸(杭三保和陆自强, 1991); 日本柄瘤蚜茧蜂寄生引起黑豆蚜中 3 种主要氨基酸中的苏氨酸含量上升(甘明等, 2003b); 川硬皮肿腿蜂寄生导致松褐天牛幼虫血

淋巴中丝氨酸、甘氨酸、丙氨酸等 10 种游离氨基酸含量或者与蛋白新生合成相关的组成氨基酸(半胱氨酸、组氨酸、谷氨酸和丝氨酸)呈现上升趋势(谭毅等, 2003)。

**寄主血淋巴蛋白质:** 寄主血淋巴内总蛋白浓度因寄生蜂的寄生而下降, 正如被二化螟盘绒茧蜂寄生的二化螟(杭三保和陆自强, 1991)、被中红侧沟茧蜂寄生的粘虫(秦启联等, 2000b)、被蝶蛹金小蜂寄生的菜粉蝶蛹(吕慧平等, 2000)、被日本柄瘤蚜茧蜂寄生的黑豆蚜(甘明等, 2003b)、被川硬皮肿腿蜂寄生的替代寄主(谭毅等, 2003)、被淡足侧沟茧蜂寄生的甜菜夜蛾(季香云等, 2013)。同时, 寄主血淋巴中涉及体液、细胞免疫和解毒等各方面蛋白的组成和丰度也会因寄生蜂的寄生而改变, 如被椰心叶甲啮小蜂寄生 0.5 d 的椰心叶甲血淋巴蛋白质中出现了 313 个与寄生相关的蛋白斑点的改变(刘奎等, 2009)、被蝶蛹金小蜂寄生柑橘凤蝶蛹血淋巴中 16 种蛋白的含量发生变化(Zhu *et al.*, 2009b)、被蝶蛹金小蜂寄生(24 h)的菜粉蝶蛹血淋巴蛋白中 masquerade-like serine proteinase、enolase、bilin-binding protein、imaginal disc growth factor、ornithine decarboxylase 和 cellular retinoic acid binding protein 等 7 个蛋白含量改变(Zhu *et al.*, 2011a)、被管氏肿腿蜂寄生黄粉甲体内 32 个蛋白的含量上调、9 个下降(Zhu *et al.*, 2013b, 2014a)。

**血淋巴糖类物质:** 寄主血淋巴内糖类物质含量因寄生蜂的寄生而上升或者下降, 其中呈现上升趋势的是: 在被蝶蛹金小蜂寄生的越冬代菜粉蝶蛹中血淋巴中总糖和海藻糖(吕慧平等, 2000)、被中红侧沟茧蜂寄生的棉铃虫幼虫糖原(李文香等, 2011)、被淡足侧沟茧蜂寄生的甜菜夜蛾血淋巴总糖(季香云等, 2013)。而呈现下降趋势的是: 被川硬皮肿腿蜂寄生的寄主体内糖原、海藻糖(谭毅等, 2003)、被日本柄瘤蚜茧蜂寄生黑豆蚜体内血淋巴海藻糖(甘明等, 2003b)。而被浅黄恩蚜小蜂 *Encarsia Sophia* (Girault-Dodd) 寄生的烟粉虱若虫体内海藻糖含量是先升高后降低, 相应的海藻糖酶活性水先

降低后升高(王颖颖等, 2015)。

**脂类物质:** 寄主脂肪体的可溶性蛋白含量和脂浓度因寄生蜂的寄生而下降, 正如被菜蛾盘绒茧蜂寄生小菜蛾(汪海燕等, 2006)、被丽蝇蛹集金小蜂寄生的棕尾别麻蝇 *Boettcherisca peregrina* (Robineau-Desvoidy) 蛹(韩成香等, 2008)、被淡足侧沟茧蜂寄生的甜菜夜蛾(季香云等, 2013)。但是甘油三酯(TAG)和其他脂类的合成酶的变化却与蛋白和脂浓度不同, 如被棉蚜茧蜂 *Lysiphlebia japonica* (Asheak) 寄生的棉蚜体内甘油三酯和其他脂类的合成酶的表达水平显著上升, 特别是甘油脂合成增加、由蔗糖代谢合成而来的柠檬酸酯减少(Zhang *et al.*, 2015; Gao *et al.*, 2017)。

**4.2.3 对寄主内分泌和生长发育的影响** 寄生蜂对寄主生长发育的影响, 第一是抑制寄主体重增长, 如中红侧沟茧蜂寄生对黏虫(Qin *et al.*, 2000b)、淡足侧沟茧蜂对甜菜夜蛾(印杨毅等, 2013)、管侧沟茧蜂对黏虫(Chu *et al.*, 2014)。第二是延长发育历期, 如被菜蛾盘绒茧蜂寄生的小菜蛾(白素芬等, 2005c; 李欣等, 2005)、被日本柄瘤蚜茧蜂寄生黑豆蚜(Gan *et al.*, 2003)。再次表现在影响寄主的变态过程, 如被菜蛾盘绒茧蜂假寄生的小菜蛾幼虫不能化蛹死亡、不能化蛹的则成为超重幼虫、能正常化蛹但不能羽化(白素芬等, 2005c), 美洲斑潜蝇幼虫被黄腹潜蝇茧蜂假寄生后虽能化蛹但无法羽化(Wan *et al.*, 2005)。如果寄生后的寄主仍然存活, 则其羽化后寿命和生殖力则受到明显的负面影响, 正如被绣线菊蚜蚜小蜂 *Aphelinus spiraecolae* Evans *et* Schauff 寄生的绣线菊蚜 *Aphis spiraecola* Patch 寿命和生殖力下降(Tang and Yokomi, 1996)、被日本柄瘤蚜茧蜂寄生的豆蚜成蚜的寿命缩短(甘明等, 2003a)。

寄生蜂对寄主生长发育和变态发育的影响归根结底是由于寄主内分泌系统受到了影响, 即保幼激素浓度由于寄生提高或蜕皮激素浓度由于寄生降低或两者皆是, 还有就是蜕皮激素受体基因转录丰度由于寄生而降低。如亚洲玉米螟卵内保幼激素酯酶 JHE 活力和蜕皮激素浓度由于

亚洲玉米螟赤眼蜂的寄生而发生改变,由此亚洲玉米螟卵的发育受到了抑制(戴华国等,2002),类似的作用还有双斑恩蚜小蜂 *Encarsia bimaculata* Heraty et Polaszek 寄生的烟粉虱(钱明惠等,2006)、蝶蛹金小蜂寄生的菜粉蝶蛹(Zhu *et al.*, 2009a)。引起内分泌激素水平发生变化的原因是寄生蜂的寄生造成内分泌腺体的结构破坏或与激素合成和释放相关的神经肽丰度发生变化。前者如注射 3-4 个寄生蜂当量的棉铃虫齿唇姬蜂病毒即可造成棉铃虫幼虫体内前胸腺退化(Zhang *et al.*, 2003),后者如菜蛾盘绒茧蜂寄生以及菜蛾盘绒茧蜂病毒则是抑制或者推后小菜蛾中枢神经内神经肽基因转录丰度(Shi *et al.*, 2015)。特别值得一提的是,菜蛾盘绒茧蜂病毒和畸形细胞能产生 miRNAs,分别通过在组织特异性转录和通过外泌体跨膜转运进入寄主组织细胞,在转录后水平上降低寄主蜕皮激素受体的含量,造成寄主幼期发育时间延长和寄主幼虫化蛹的推迟,实现了 miRNAs 跨物种的发育调控(Wang *et al.*, 2018)。

**4.2.4 对寄主生殖的影响** 对寄主生殖系统的影响目前报道于雄性寄主精巢(生殖系统)中。菜蛾盘绒茧蜂和半闭弯尾姬蜂寄生都能抑制雄性寄主幼虫精巢的增大、对精巢中精母细胞的结构产生破坏作用以至于无正常精子出现,还能降低精巢总蛋白含量,但前者造成寄主精子束畸形,后者造成精巢畸形,且前者的抑制作用强于后者(蔡东章等,2006;何璠等,2009; Bai *et al.*, 2009)。

**4.2.5 对寄主抗逆性的影响** 寄主生理内环境由于寄生发生课明显的变化,相应的多种与抗逆相关的酶也发生了改变,主要是活力上升为多。如切割潜蝇茧蜂的寄生提高橘小实蝇幼虫体内过氧化物酶(POD)的活性(梁光红等,2007c);椰甲截脉姬小蜂对椰心叶甲的寄生可以提高寄主幼虫体内过氧化氢酶(CAT)、过氧化物酶、酯酶(EST)活性(宋晓君等,2009)。这些抗逆性相关酶活力上升是由于相关基因转录丰度的升高,如管氏肿腿蜂寄生后的黄粉甲体内超氧化物歧化酶(SOD)基因转录丰度的升高(Zhu

*et al.*, 2014b)。与之相反的情况也存在,正如菜粉蝶蛹的 *hsp75* 和 *hsp90* 转录丰度由于蝶蛹金小蜂的寄生而下降,相应的抗逆性也会下降(Zhu *et al.*, 2013a)。

**4.2.6 对寄主行为的影响** 国内外对寄生蜂寄生导致寄主行为发生改变的研究报道并不常见,总结国内已有研究发现寄生蜂寄生对寄主行为的影响主要在取食和栖境的选择上。正如小菜蛾幼虫的取食行为由于菜蛾盘绒茧蜂和半闭弯尾姬蜂的寄生而受到抑制(Shi *et al.*, 2002; Huang *et al.*, 2008a);又如滞育中红侧沟茧蜂的寄生能驱使寄主幼虫移动到接近土壤的低处植物叶片背面而非滞育的中红侧沟茧蜂的寄生则驱使寄主幼虫攀爬到寄主植物高处的叶片背面(Luo *et al.*, 2013b),这也说明寄生蜂对寄主行为的影响也受到自身生理状态的影响。

## 5 寄生蜂的人工繁殖

### 5.1 替代寄主

寄生蜂的人工繁殖首先需要解决的问题是找到易于生产并接近原有寄主适宜程度的替代寄主。我国成功的实践就是赤眼蜂的人工繁育。最初的实践是1936年祝汝佐和胡永锡筛选出14种、蒲蛰龙等则筛选出16种鳞翅目昆虫的卵可被赤眼蜂寄生(张俊杰等,2015)。在不断的实践过程中,首先获得成功的是利用柞蚕卵繁殖赤眼蜂(即“大卵繁蜂”)。从柞蚕卵中培育出的玉米螟赤眼蜂寄生亚洲玉米螟卵的能力是从米蛾卵中培育出来的2倍(Liu *et al.*, 1998);跳小蜂雌蜂个体显著大于从自然寄主舞毒蛾卵繁育出的雌蜂个体(王建军等,2012)。但是长期人工大量繁殖赤眼蜂的过程中发现,除了松毛虫赤眼蜂和螟黄赤眼蜂等少数种类外,多数赤眼蜂不能在柞蚕等体积较大卵中产卵,只能在如米蛾、小菜蛾、甜菜夜蛾这些体积较小的卵中产卵(邸宁等,2018),所以,小卵作为替代寄主进行赤眼蜂的大量繁育这一新的模式随之就发展起来;但因小菜蛾等昆虫卵因不易收集、育出赤眼蜂后代雌性比率低和种性退化严重等各种问题,米蛾

卵成为了第一选择(张俊杰等, 2015)。因此, 米蛾的人工饲养技术、卵的保存技术和利用米蛾卵繁育各类赤眼蜂以及子代的品质的研究、工厂化繁育配套设备和技术流程在很大程度上就广泛开展起来。目前, 利用螟黄赤眼蜂、稻螟赤眼蜂、玉米螟赤眼蜂、松毛虫赤眼蜂等各种人工繁育获得的赤眼蜂防治松毛虫、甘蔗螟虫、玉米螟、棉铃虫、烟青虫 *Helicoverpa assulta* Guenée、二化螟、稻纵卷叶螟等多种农林害虫(张俊杰等, 2015; 徐红星等, 2017)。

除了赤眼蜂之外, 其它较为成功寄生蜂替代寄主繁育的还有利用意大利蜜蜂 *Apis mellifera ligustica* 雄蛹繁殖管氏肿腿蜂(姚万军和杨忠歧, 2008)、黄粉甲 *Tenebrio molitor* Linnaeus 蛹繁育管氏肿腿蜂(代平礼等, 2005)、粘虫繁殖棉铃虫齿唇姬蜂(Zhang *et al.*, 2010a)、柞蚕卵繁育大蛾卵跳小蜂 *Ooencyrtus kuwanae* (Howard)(王建军等, 2012)、柞蚕卵繁育白蛾黑基啮小蜂 *Tetrastichus nigricoxae* Yang(郭同斌等, 2012)、黑腹果蝇 *Drosophila melanogaster* Meigen 繁殖家蝇 *Musca domestica* L. 的蛹寄生蜂(周和锋等, 2014)、杨十斑吉丁虫 *Melanophila picta* Fabricius 幼虫繁育落叶松吉丁肿腿蜂 *Sclerodermus* sp.、白蜡吉丁肿腿蜂和管氏肿腿蜂这 3 种寄生蜂(牛春林等, 2015)、柞蚕卵繁育舞毒蛾卵平腹小蜂(刘鹏程等, 2015)、大豆蚜 *Aphis glycines* Matsumura 繁育白足蚜小蜂 *Aphelinus albipodus* Hayat *et Fatima* (Song *et al.*, 2017)、柞蚕卵繁育白蛾周氏啮小蜂(孙静, 2019)等等。

不同寄主/寄生蜂比率对寄生蜂的繁育具有显著影响。以黄粉虫为替代寄主繁殖管氏肿腿蜂人工扩繁时, 寄主和雌蜂比为 2:1 较适宜(代平礼等, 2005), 而以青杨天牛繁育管氏肿腿蜂时则是 4-5:5(周娜等, 2006)。由于对单寄生蜂生长发育不利的过寄生现象普遍存在于单寄生蜂寄生过程中(李元喜等, 2001; 江化琴等, 2014), 所以在大量繁殖如菜蛾盘绒茧蜂和螟蛉盘绒茧蜂 *Cotesia ruficrus* (Haliday) 等的单寄生蜂时, 应减少接蜂密度和接蜂时间。寄生蜂还会通过生殖调整来应对缺乏寄主的情况, 如羽化后

4 日内的卷蛾分索赤眼蜂对于短期缺乏寄主适应性较强, 在恢复供寄主卵首日会提高寄生卵量, 且这种调整对成蜂自身的繁殖力和成虫寿命没有明显影响(陈科伟等, 2002)。

## 5.2 补充营养

寄生蜂成蜂搜索、交配、寄生等活动所消耗的能量需要由取食营养物质(主要是碳水化合物)来补充, 所以碳水化合物对寄生蜂成蜂的存活、繁殖力(寄生力)和后代性比有直接影响(宋南等, 2006)。取食蜂蜜、玉米花粉、褐飞虱蜜露和大豆花粉均能明显延长稻虱缨小蜂成蜂的寿命和提高对褐飞虱卵的寄生能力(郑许松等, 2003)。取食 20% 蜂蜜水+酵母粉的切割潜蝇茧蜂雌蜂能产更多的卵(梁光红等, 2007a)。无补充营养(饥饿)的蝶蛹金小蜂雌蜂总体产卵量减少(Dong *et al.*, 2008)。类似补充营养显著延长雌蜂寿命和提高产卵量的研究还涉及豌豆潜蝇姬小蜂 *Diglyphus isaea* Walker(Zhang *et al.*, 2011)、蝇蛹金小蜂(Hu *et al.*, 2012)、芙新姬小蜂 *Neochrysocharis formosa* (Westwood)、(Wang *et al.*, 2014)、海氏桨角蚜小蜂(Zhang *et al.*, 2014)等。

## 5.3 低温贮藏

长期保存而不降低寄生蜂活力是规模化繁殖寄生蜂的重要技术之一, 也是高效利用寄生蜂进行生物防治的前提和保障。虽然较低的温度可以延长寄生蜂的贮藏时间, 但对适合度会产生不利影响(Shi *et al.*, 2013a), 因此研究和筛选最佳贮存低温度和时间对于寄生蜂的规模化生产和随后的运输和应用至关重要。目前利用低温处理寄主、低温处理已被寄生蜂寄生的寄主和低温处理寄生蜂, 随后进行评估, 获得了最佳保存温度和时间(陈倩等, 2006, 2007, 2008a, 2008b; 胡镇杰等, 2017)、椰心叶甲啮小蜂(Liu *et al.*, 2014a; Tang *et al.*, 2014)、冷冻蝇蛹与丽蝇蛹集金小蜂和蝶蛹金小蜂繁育(张忠等, 2009a, 2009b; 贺张等, 2013)、米蛾卵与赤眼蜂(Huang *et al.*, 2017)、僵蚜与烟蚜茧蜂(唐文颖等, 2011; 宋

修超等, 2012; 夏诗洋等, 2013)。也可以在保证有充足补充营养、相对低温的条件下, 通过短时间内降低成蜂的活动而延长成蜂寿命的方式直接保存寄生蜂成虫, 如丽蝇蛹集金小蜂(任倩等, 2011)、麦蛾柔茧蜂(Chen *et al.*, 2011b, 2013)等。

#### 5.4 滞育调控

滞育状态的寄生蜂可以比非滞育状态的在冷库中存活的时间更长, 诱导寄生蜂进入滞育, 在延长贮存时间和货架期、调节释放羽化时间以适时防治、加强和促进抗逆性和繁殖力等方面具有积极意义。滞育的寄生蜂不仅存活久且对不良环境适应性强所以更容易保存。如在 5 °C 条件下保存不同周数的麦蛾柔茧蜂雌蜂, 其滞育的雌蜂存活率、寿命、产卵量、卵的孵化率等各类指数都明显高于未滞育(Chen *et al.*, 2013)。据统计, 近 70 年来全世界共有 128 种寄生蜂做过滞育特性研究(张礼生等, 2014a), 其中我国研究人员研究的寄生蜂有 16 种, 即寄生松毛虫属 *Dendrolimus* 害虫的枯叶蛾平腹小蜂 *Anastatus ramakrishnai* (Mani) 和松毛虫赤眼蜂、寄生棉蚜的异足蚜小蜂 *Aphelinus varipes* (Foerster)、寄生美国白蛾的白蛾周氏啮小蜂、寄生白蜡窄吉丁的白蜡吉丁柄腹茧蜂、寄生三化螟 *Scirpophaga incertulas* (Walker) 的螟卵啮小蜂 *Tetrastichus schoenobii* Ferriere、寄生细蛾科 Gracilariidae 的细蛾多胚跳小蜂 *Holcothorax testaceipes* (Ratzeburg)、寄生玉米螟 *Pyrausta nubilalis* (Hubern) 的亚洲玉米螟赤眼蜂、寄生双色泉蝇 *Pegomya bicolor* (Wiedemann) 的双色泉蝇茧蜂 *Biosteves* sp.、寄生夜蛾科低龄幼虫的中红侧沟茧蜂、寄生烟蚜的烟蚜茧蜂、寄生麦蛾 *Sitotroga cerealella* (Olivier) 的麦蛾柔茧蜂、寄生丽蝇科 Calliphoridae 和麻蝇科 Sarcophagidae 的丽蝇蛹集金小蜂、寄生小菜蛾的菜蛾盘绒茧蜂、寄生甜菜夜蛾、斜纹夜蛾和粘虫的管测沟茧蜂、寄生草地螟的草地螟阿格姬蜂 *Agrypon flexorium* (Thunberg) (张礼生等, 2014a; 张洪志等, 2018)。上述研究表明, 寄生蜂的滞育虫

态有老熟幼虫、预蛹、蛹和成虫, 其中以老熟幼虫和预蛹滞育为多(各分别有 7 种和 8 种)。由于滞育的敏感阶段常为滞育虫态的前一虫期, 即对其进行诱导滞育的最佳时期, 就可以获得进入滞育的种群。如: 将柞蚕卵中松毛虫赤眼蜂新产的卵在 26 °C 保存 40 h 后转入 10 °C 诱导 4 周是诱导松毛虫赤眼蜂滞育的最佳方法(Ma and Chen, 2006); 用低温和短日照处理发育阶段为卵或者 1 龄幼虫的草地螟阿格姬蜂就能诱导其在老熟幼虫阶段进入滞育(徐忠宝等, 2013), 而用低温和短日照处理发育阶段为 2 龄幼虫的中红侧沟茧蜂则诱导其在预蛹阶段进入滞育(浑之英等, 2005; Li *et al.*, 2008); 白蛾周氏啮小蜂属长日照型昆虫, 以老熟幼虫进入滞育状态, 在幼虫阶段诱导其进入滞育的临界光周期会因为饲养的温度上升而缩短(孙守慧等, 2009); 对麦蛾柔茧蜂来讲, 在 20 °C 或者 17.5 °C 这两个温度、光照周期分别为 16、13 或 10 h 的条件下生长的幼蜂发育至成虫后, 在光照时间为 10 h 条件下育出的雌蜂都能进入生殖滞育(Chen *et al.*, 2012)。

除了温度和光周期外, 影响寄生蜂滞育的因素还主要有亲代情况(即亲代效应)以及所处的地理环境。亲代的滞育特征会影响子代的表现型即为滞育的亲代效应, 一般昆虫的滞育亲代效应多为母代对子代滞育的影响, 寄生蜂也不例外; 同时, 寄生蜂的滞育的亲代效应除了受亲代自身因素等的影响外, 还受滞育持续时间、光周期、温度等环境条件的影响(张礼生等, 2014a)。母代经历的光周期对子代的滞育有显著影响, 甚至完全决定其子代的滞育, 亲代会根据自身经历的光周期而决定其子代是否进入滞育或者进入滞育的条件和滞育比例。如在长日照条件下饲养亲代菜蛾盘绒茧蜂可降低子代滞育诱导的临界温度(郭玉玲等, 2007); 滞育亲代烟蚜茧蜂所产下的子蜂滞育率和非滞育亲代所产下的子蜂相比, 由对照的 44.75% 提高至 74.01% (张礼生等, 2014b)。处于不同地理环境的寄生蜂种群可能发生遗传分化, 而分化的寄生蜂种群之间的滞育诱导条件和滞育率之间存在显著差异, 如在中国

3 个不同地区的松毛虫赤眼蜂种群(黑龙江、辽宁和江苏)中,来自于黑龙江和辽宁种群的滞育诱导临界温度和滞育率要显著高于来自于江苏的(Zhang *et al.*, 2017a)。

需要注意的是处于滞育状态的寄生蜂仍需进行代谢和消耗,所以过长的滞育期会对寄生蜂产生不利影响,这从滞育寄生蜂体内的代谢组与非滞育的不同看出。如滞育的丽蝇蛹集金小蜂体内的有包括三羧酸循环和糖异生在内的 22 条代谢通路发现改变和富集,特别是糖酵解产物增多与滞育蜂耐寒性的提高相吻合(Li *et al.*, 2015);处于滞育期的烟蚜茧蜂体内有 278 个蛋白质的含量显著上升(黄凤霞等, 2015),其中很多是在非滞育阶段不表达或者微量表达的滞育关联蛋白(张礼生等, 2015)。菜蛾盘绒茧蜂滞育蛹中的氧化物歧化酶活性上升而过氧化氢酶活性下降,其子代卵的氧化物酶和过氧化氢酶活性均明显上升说明滞育亲代效应能延伸到子代的抗逆特性上(Hao *et al.*, 2012)此外,寄主的营养状态也间接影响寄生蜂的滞育,如寄主饲料中某些氨基酸浓度过高会导致滞育蜂体内必需氨基酸浓度升高、代谢物与能源利用率减少、脂质和氨基酸代谢紊乱的现象(Li *et al.*, 2015)。

一般昆虫滞育的解除是光周期和温度的变化,寄生蜂也是如此,但是喷施适宜浓度的有机溶剂可以有效促进寄生蜂滞育的解除,并显著缩短滞育解除蜂羽化历期、提高羽化整齐度(侯艳红等, 2011),利于在生物防治中的释放应用(Zhang *et al.*, 2014)

## 5.5 其他因素

依据寄生蜂产卵具有明显偏好性和选择性的特性,在人工繁殖寄生蜂的过程中可以通过使用产卵增效剂或者改变物理或生物因素促进寄生蜂雌蜂在替代寄主上产卵。在利用人工卵繁殖赤眼蜂时,可使用的产卵增效剂有聚乙烯醇、明胶、白乳胶、琼脂、木薯粉、米粉和淀粉等去刺激松毛虫赤眼蜂、拟澳洲赤眼蜂 *T. confusum* Viggiani 及广赤眼蜂 *T. euanescens* Westwood 产卵(Han *et al.*, 1994),或者使用与寄主幼虫血淋巴卵液中的同类、浓度接近的钾离子、镁离子

和钠离子等阳离子溶液人工卵刺激雌蜂产卵(Nettles *et al.*, 1985)。阿里山潜蝇茧蜂 *Fopius arisanus* (Sonan) 对生长在琼脂含量为 2% 的产卵盘中寄主有最大的寄生率(耿军灵等, 2009)。辐射处理寄主卵(改变寄主卵的适合度)或者寄生蜂雌蜂(刺激生殖)都可以刺激寄生蜂雌蜂的产卵,正如用 300 Gy  $\text{Co}^{60}$  处理新产(<8 h)寄主棉铃虫卵或者 250 Gy 处理雌蜂都可以提高玉米螟赤眼蜂的繁殖率(Wang *et al.*, 2009a),在分别用 20Gy 辐射 6 h 和 30-36 h 的桔小实蝇卵中培育出来的长尾全裂茧蜂(Cai *et al.*, 2018)和阿里山潜蝇茧蜂(Cai *et al.*, 2017)综合表现都较好。

## 6 生物防治技术与策略

### 6.1 寄生蜂的人工释放

**6.1.1 单种天敌释放** 田间寄生蜂释放是天敌在生物防治应用过程中核心环节,在我国已有的利用多种赤眼蜂防治螟虫类害虫、平腹小蜂 *Anastatus japonicus* 防治荔枝蝽象 *Tessaratoma papillosa* (Drury)、中红侧沟茧蜂防治棉铃虫、周氏啮小蜂防治美国白蛾、肿腿蜂防治天牛、啮小蜂防治椰心叶甲的生物防治实践过程中,对单种寄生蜂释放过程中的关键技术进行了研究,有效提高了寄生蜂应用的效率,并为寄生蜂在相关害虫可持续的生物防治过程中的长期应用提供了保障。

平腹小蜂是荔枝蝽象的优势卵寄生蜂,我国广东、福建等荔枝产区一直利用平腹小蜂防治荔枝蝽象,现今平腹小蜂的释放已形成了完整的田间释放技术体系,先于荔枝蝽的产卵始盛期进行第 1 次放蜂,再于 10-12 d 后释放第 2 次,即能达到防治荔枝蝽的最佳效果,且整个荔枝花期无需再使用杀虫剂,对虫媒昆虫的活动和荔枝园的生境起到良好的保护作用(余春仁等, 1997)。中红侧沟茧蜂能寄生棉铃虫、粘虫、小地老虎等鳞翅目夜蛾科 5 个属的低龄幼虫,自 1979 年被河北省农林科学院植物保护研究所发现以来,在开展其生物学特性、发生消长规律、人工饲养、化学生态学等方面的研究基础上进行大规模释

放技术探索,最终在新疆棉田的释放量为 7 500-15 000 头/hm<sup>2</sup>,从棉铃虫卵孵化盛期开始释放 1-2 次即可有效控制棉铃虫为害,减少为害损失 80%以上,而在玉米和露地蔬菜地中分别释放 1 次和 2 次对玉米田 3 代棉铃虫幼虫寄生率分别达到 51.22%和 60.35%以及防治效果分别为 68.42%和 77.63% (李建成等, 2010)。

针对入侵性林业重大害虫松突圆蚧,本地天敌调查和筛选后发现 3 种本地优势寄生蜂-长缨盾蚧丽蚜小蜂 *Encarsia citrina* Craw、爱友丽蚜小蜂 *E. amacula* Viggiani et Hui 和范氏黄小蜂 *Aphytis vandenboschi* DeBach et Rosen,在室内利用马铃薯、南瓜和柠檬等果实饲养的茶钹盾蚧 *Abgrallaspis cyanophylli* (Signoret)、夹竹桃蚧 *Aspidiotus nerii* (Signoret) 和红圆蚧 *Aonidiella aurantii* (Maskell) 作为替代寄主,进行了大量繁殖后,分别在广东番禺南沙、增城林场白水工区、阳东县合水镇等地的松突圆蚧发生区进行放蜂试验,结果表明这 3 种寄生蜂均可在林间定殖,其中范氏黄小蜂是所释放 3 种寄生蜂中对松突圆蚧雌蚧的寄生率最高,可达到 10.92% (比对照提高 5.62%),能在生物防治松突圆蚧过程中发挥重要作用 (何国锋等, 1995)。花角蚜小蜂是从原产地引入的控制松突圆蚧为害的寄生蜂,在福建地区释放后取得了一定的效果,该蜂的释放在时空间上应多点 (间隔 100-200 m) 放蜂,在时间上应周期性 (间隔 4-5 年) (陈顺立等, 2011)。白蛾周氏啮小蜂是入侵昆虫美国白蛾在我国本地优势寄生蜂种类,围绕白蛾周氏啮小蜂应用的研究已较为深入,目前已形成了一套相对成体系的林间释放技术,即一般采用直接挂树法或直接利用茧孔悬挂在树杈上进行林间释放,放蜂量则根据美国白蛾的数量确定,发生严重地区的蜂虫比 3 : 1 为宜,气温在 25 °C 以上释放比较容易达到理想的防治效果,同时由于美国白蛾世代不整齐、化蛹持续时间较长,每年需放蜂 4 次 (郑雅楠等, 2012)。最近,在沈阳市美国白蛾发生区,蒙古栎、刺槐、黄波罗等树种较多的林地进行释放的研究结果表明,各试验区 7 月份和 9 月份的有虫株率分别比对照下降了

32.1%和 40.0%,平均网幕密度分别比对照每株降低 3.5 网和 5.4 网,9 月份有虫株率和网目密度均比 7 月份有所减少,说明仅单次独立释放白蛾周氏啮小蜂就能有效地防治美国白蛾的为害,但是连续 2 次放蜂效果会更好 (郝常华, 2019)。烟粉虱在我国的天敌资源也很丰富,研究和探索其优势寄生蜂天敌释放和防治效果,一直都是烟粉虱综合防治的研究热点。桨角蚜小蜂是烟粉虱的优势寄生蜂之一,在黄瓜大棚探讨了不同放蜂密度的控制效果,获得了按作物植株树为基础的最佳放蜂密度 (3-5 头雌蜂/植株) (邱宝利等, 2004); 丽蚜小蜂自引入我国后,结合我国现有日光温室-保护地的特点,形成了在设施蔬菜环境下释放丽蚜小蜂控制害虫烟粉虱的技术,即在设施蔬菜上烟粉虱发育至 2-3 龄若虫时即可释放丽蚜小蜂 (益害比为 1 : 30-50,每 667 m<sup>2</sup>一般释放 5 000-10 000 头),每隔 7-10 d 释放 1 次、连续释放 3-4 次即可 (张君明等, 2010)。

**6.1.2 多种天敌联合释放** 为了提高对某一种害虫的防控效率,在寄生蜂的实际应用过程中也会进行“多种天敌组合释放”,包括不同种寄生蜂的组合释放、寄生蜂与捕食性天敌的混合释放以及寄生蜂与微生物的联合应用。如在烟粉虱的防治过程中按 3 : 1 的比例释放海氏桨角蚜小蜂和浅黄恩蚜小蜂这两种寄生蜂能获得对烟粉虱防治的最佳效果 (Xu et al., 2015; 张晓明等, 2018); 捕食性天敌东亚小花蝽 *Orius sauteri* (Poppius)、异色瓢虫 *Harmonia axyridis* (Pallas) 分别与丽蚜小蜂、浅黄恩蚜小蜂一起释放时,和单独释放或仅寄生蜂混合释放相比,寄生蜂均能寄生更多的烟粉虱 (李姝等, 2014; Tan et al., 2016b); 同时释放丽蚜小蜂和浅黄恩蚜小蜂时,虽然每一种寄生蜂对烟粉虱若虫的寄生率都比单独释放的低,但烟粉虱的总死亡率增加 (Pang et al., 2011)。在桑天牛 *Apriona germari* (Hope) 的防治过程中进行了将虫生真菌与寄生蜂联合施用,发现接种过球孢白僵菌 *Beauveria bassiana* 的管氏肿腿蜂对桑天牛的寄生效率更高 (Li et al., 2017a)。在利用微生物农药防治印度谷螟的同时释放的麦蛾茧蜂会对 Bt 制剂对印度谷螟

的致死作用起叠加效应 (Oluwafemi *et al.*, 2009)。结合雄性不育技术、性诱剂和阿里山潜蝇茧蜂防治橘小实蝇研究发现, 先利用性引诱剂降低田间橘小实蝇雄虫数, 随后释放不育橘小实蝇雄虫以进一步降低种群数量, 最后在前两者基础上释放阿里山潜蝇茧蜂寄生橘小实蝇以对种群数量起到持续控制作用, 最终总体防治效果可达 90% 左右 (郑思宁等, 2013)。在我国海南岛田间自然条件下, 虽然在单独释放椰甲截脉姬小蜂和椰心叶甲啮小蜂这两种寄生蜂都可以降低椰心叶甲的虫口密度, 但是效果明显低于混合释放的, 所以, 目前按“保持椰甲截脉姬小蜂的释放数量是椰心叶甲啮小蜂的 3 倍且蜂总量是椰心叶甲数量的 10 倍, 连续释放 4-5、每次放蜂间隔期为 1 个月”的技术要点释放寄生蜂能完全有效控制椰心叶甲的为害 (金涛等, 2012)。

值得注意的是, 不同种寄生蜂的组合释放防治同一种害虫的时候, 在考虑到不同寄生蜂的寄生特点情况下也能显著提高总寄生率, 正如同时释放寄生蜂 *Psytalia incis* 和阿里山潜蝇茧蜂防治橘小实蝇总出蜂率略高于单独释放其中任何一种寄生蜂 (Yang *et al.*, 2018a)、同时释放稻螟赤眼蜂和松毛虫赤眼蜂防治水稻二化螟 (卵) (杜文梅等, 2016)。

## 6.2 寄生蜂的保护和助增

农田生态系统是以农作物为核心人为地改造而建立起来的生态系统, 通常是大面积种植单一品种的作物, 所以系统中植被较单纯、生物多样性也较低, 而农田生态系统生物多样性的下降与害虫的频繁暴发直接相关。昆虫学家和生态学家根据他们的研究工作提出采用合理的耕作制度和栽培措施可以保护和强化农田生物多样性, 从而有利于充分发挥寄生蜂等自然天敌的生物控害作用 (尤民生等, 2004)。

**6.2.1 作物间作** 作物间作和轮作是害虫防治过程中农业生境管理常用的手段, 不同功能类型作物的合理配置而非单一的、强调植物的多样化是目前保护性生物防治的研究重点之一。科学种植不同功能植物是提高生物控害作用、增加农业

生态系统的服务价值的重要方法 (赵紫华等, 2013)。

小麦是我国重要的粮食作物, 占我国粮食产量的五分之一, 而蚜虫是小麦上最主要的害虫, 繁殖速度快、直接取食植物汁液并传播多种植物病毒, 造成小麦产量和品质的重大损失, 所以我国科研人员在各个小麦产区围绕生物防控小麦蚜虫进行了间套种作物研究。目前筛选获得有效的间套作植物种类有油菜、蚕豆、豌豆和荷兰豆, 和小麦单作相比, 随着系统中物种多样性的增加, 蚜虫寄生蜂天敌种群得到了保护, 最终僵蚜率和蜂/蚜比也显著升高 (王万磊等, 2008; Wang *et al.*, 2009b; 李川等, 2011; 费晓东等, 2012; Xie, 2012; Zhou *et al.*, 2013)。同一作物不同抗性品种的混作具有类似的天敌保护功能, 正如北京 837 单作或与另外 4 个小麦品种间作后, 其蚜茧蜂 (燕麦蚜茧蜂 *Aphidius savenae* Haliday、烟蚜茧蜂) 的平均数量增加 (周海波等, 2009)。与小麦相似, 大田作物类似玉米、棉花都可以进行不同作物的间套作, 通过间套作增加天敌数量以防治主作物上的害虫。如在广西壮族自治区增城市进行玉米田间套作绿豆通过提高玉米螟赤眼蜂对亚洲玉米螟卵的数量和寄生率以防治玉米螟 (周大荣等, 1997a, 1997b; 田耀加等, 2012)。在云南滇西南地区, 玉米田间套作甘蔗可显著增加亚洲玉米螟的 3 种主要寄生蜂-螟蛉绒茧蜂 *Apanteles ruficrus* Haliday、黄眶离缘姬蜂 *Trathala flavoorbitalis* Cameron 和大螟钝唇姬蜂 *Eriborus terebrans* Gravenhorst 的种群密度, 显著降低亚洲玉米螟卵块密度与卵粒密度、蛀孔密度与百秆虫量 (陈斌等, 2015)。在云南普洱轮作小麦、萝卜等作物以及邻作茶叶的玉米田中寄生蜂群落的比例显著高于单种玉米的, 同时寄生蜂群落上升成为主导整个生态体系内总节肢动物群落的变化因子之一 (柴正群等, 2016)。在河北邯郸地区转基因棉田中, 间作不论是抗或者感麦长管蚜的冬小麦品种都可以比单种棉花更保存和增强寄生蜂种群从而减少棉蚜的虫口数量 (Ma *et al.*, 2006)。在大豆田间作甜葫芦、香瓜、烟草和玉米等经济作物, 与单作大豆田相比,

大豆蚜虫种群数量降低了 40.7%以上,由此大豆田中寄生蜂与蚜虫的益害比明显提高(李新民等, 2014)。

在蔬菜生态系统中,间套种不同蔬菜种类和品种,也起到趋避或诱集作用,增强寄生蜂等天敌昆虫的控害功能。在福建省琅岐岛的小白菜田间/套作大蒜,发现间作大蒜可以提高田间寄生蜂的丰盛度和数量(蔡鸿娇和尤民生, 2007)。在花椰菜田间作番茄(株数占花椰菜总株数比 10%、30%、50%)不仅提高了菜蛾盘绒茧蜂的个体数量和蜂/蛾比,还降低了另外两种害虫-菜蚜、黄曲条跳甲的数量(夏吁等, 2015)。在辣椒田地间种甘蔗能显著提高南美斑潜蝇的几种优势寄生蜂-豌豆潜蝇姬小蜂、潜蝇茧蜂 *Opius* sp.、异角短胸潜蝇姬小蜂 *Hemiptarsenus varicornis* (Girault) 的个体数量和它们对南美斑潜蝇的寄生率(Chen *et al.*, 2011a)。近年来随着温室(保护地)蔬菜栽培面积逐步增加且生态环境趋于稳定、有利于各种害虫的增殖,所以在温室(保护地)蔬菜害虫的防治过程中特别重视对植物的挥发性气味的研究并由此进行间套种作物种类的筛选。如依据气相色谱法对芹菜气体挥发物主要成分的分析结果,在保护地番茄或保护地黄瓜种植区间作芹菜,发现对温室白粉虱和烟粉虱的驱避效果分别达到 98.0%和 84.5%(朱培祥等, 2011)。

水稻生态系统相对较为特殊,其他粮食作物或者经济作物的间作和轮作主要在稻田区外(即邻作)也会对稻田内寄生蜂产生影响。在稻田边的设置茭白田,利用茭白 *Zizania latifolia* 上长绿飞虱 *Saccharosydne procerus* Matsumura 繁殖稻虱缨小蜂进而达到控制水稻田中稻飞虱的目的(俞晓平等, 1999; 郑许松等, 1999)。在水稻田边埂堤坝种植大豆则可以丰富水稻生态系统的生物多样性,不仅降低了褐飞虱的种群丰度还能促进寄生蜂向稻田中的迁移由此提高了天敌寄生蜂和害虫的比例,最终稻田中螟虫和飞虱各个阶段的寄生率都显著上升(Yao *et al.*, 2012; 戈林泉等, 2013)。

果园生态系统与其他作物生态系统相比,表

现为单一果树的生长期长,园内科学种植非果树类植物则更利于有天敌昆虫的繁殖。比如,有目的地套种以豆科牧草为主的绿肥作物为寄生蜂提供繁衍、活动和化学防治害虫时的躲避场所,有利于果园寄生蜂繁衍和形成稳定的种群。如在北京门头沟苹果园内的果树行间混种植紫花苜蓿和/或黑麦草,和对照清耕区相比,蚜小蜂、跳小蜂 *Aphidencyrthus aphidivorus* (Mayr.) 等寄生蜂的发生期显著提高,且总量和密度显著增长(迟全元等, 2011)。若结合绿肥作物,进一步在果园设置种有益杂草的生草园,则可以进一步显著增加寄生蜂的数量。正如行间种植有紫花苜蓿的苹果树搭配引入夏至草、泥胡菜等有益杂草的生草园后,苹果园中主要害虫之一的金纹细蛾 *Lithocolletis rignoniella* Mats.被金纹细蛾跳小蜂 *Ageniaspis pestacipes* Rate.、金纹细蛾姬小蜂 *Sympiesis laevifrons* Kamijo 和金纹细蛾绒茧蜂 *Apanteles theivora* Mina.这 3 种寄生蜂寄生的联合寄生率分别是免耕园、清耕稀植园和清耕密植园的 1.34 倍、16.9 倍和 17.9 倍(于毅和严毓骅, 1998; 张金钰等, 2012)。在苹果树行间作芳香植物(紫花藿香蓟 *Ageratum houstonianum*、孔雀草 *Tagetes patula* 和夏香薄荷 *Satureja hortensis*)可以增加果园内赤眼蜂科、姬蜂科、茧蜂科天敌的密度,由此降低了卷蛾科害虫(苹果小卷叶蛾 *Adoxophyes orana* Fisher、芽白小卷蛾 *Spilonota lechriaspis* Meyrick 和黄斑卷蛾 *Acleris fimbriana* Thunberg)种群的增长速度和密度(Song *et al.*, 2014)。在梨园中间作同样的芳香植物也能得到类似的效果(Song *et al.*, 2010)。目前,茶叶的无公害生产和有机生产已成为茶园发展的重要方向,而茶园虫害防治是有机茶生产的关键环节之一,目前间作在茶园生态系统中发挥着和在其他农业生态系统一样作用。在茶树间作罗勒 *Ocimum basilicum* 或紫苏 *Perilla frutescens* 可以显著增加寄生蜂的总量和密度(张正群等, 2016); 间作铺地木兰 *Indigofera endecaphylla*+ 罗顿豆 *Lotononis bainesii*、圆叶决明 *Chamaecrista rotundifolia* + 白三叶 *Trifolium repens*、白三叶+平托花生 *Arachis pintoi* 这 3 种

不同组合绿肥, 不仅能提高茶园寄生蜂在茶园冠层群落的比率, 而且寄生蜂对害虫的空间数量跟随效应强 (李慧玲等, 2016)。

**6.2.2 种植蜜源植物** 补充营养是促进寄生蜂雌蜂的生殖系统, 特别是卵巢发育成熟的重要营养物质, 可以提高寄生蜂的生殖力、存活率、搜索能力和寄生能力, 而显花植物的花蜜和花粉则是田间寄生蜂补充营养的主要来源, 所以种植蜜源植物是一种提高生物防治效果的有效手段, 近年来在我国生物防治过程中开始广泛应用 (陈学新等, 2014)。不同的显花植物由于其花蜜营养成分不同对寄生蜂的影响也不同 (朱平阳等, 2012)。对 23 种植物的筛选和测试表明, 芝麻 *Sesamum indicum* 是一种有效的蜜源植物, 稻虱缨小蜂取食芝麻花蜜后寿命延长约 30%, 对寄主卵寄生率显著上升, 且平均处置时间从 31.29 min 降低到 18.36 min (Zhu *et al.*, 2013c)。在浙江省金华市水稻田边种植芝麻可以提高稻飞虱和稻纵卷叶螟寄生蜂的数量, 田间调查表明在田埂种植芝麻的生态控制区 (不使用化学杀虫剂) 的稻飞虱寄生蜂数量是农民自防田的 4-10 倍, 稻飞虱数量显著降低 12 倍 (吕仲贤等, 2008; 朱平阳等, 2012, 2015; Gurr *et al.*, 2012; Zhu *et al.*, 2015a, 2018b), 且在中、泰、越三国水稻种植区长达 4 年的应用结果进一步说明了该技术体系对寄生蜂群落功能和控害效果有促进作用 (Gurr *et al.*, 2016)。车轴草 (又称三叶草) 和酢浆草 *Oxalis corniculata* 花期最长可达 200 d, 花蜜中含有丰富的碳水化合物 (葡萄糖、果糖以及少量蔗糖), 水稻田埂种植这 2 种显花植物能显著延长和提高螟虫卵寄生蜂-螟黄赤眼蜂的寿命和寄生力, 是优良的蜜源植物 (赵燕燕等, 2017)。除花蜜碳水化合物组成外, 显花植物的花色对寄生蜂也有影响。螟黄赤眼蜂对不同颜色的瓜叶菊 *Senecio cruentus* 花的选择性研究表明, 螟黄赤眼蜂趋向于亮度高颜色 (白色和粉红色) 的花 (汪庚伟等, 2015)。

在蔬菜生态系统中种植蜜源植物也取得了同样的效果。以甘蓝产区中小菜蛾、棉铃虫、甜菜夜蛾、斜纹夜蛾、粘虫、亚洲玉米螟、草地螟

7 种重要的蔬菜害虫和中红侧沟茧蜂、浅黄恩蚜小蜂、瘤侧沟茧蜂和蝶蛹金小蜂 4 种寄生蜂为对象进行了实验测试, 结果表明芝麻蜜源对蝶蛹金小蜂和浅黄恩蚜小蜂这 2 种寄生蜂的雌蜂寿命有显著的延长作用, 对小菜蛾成虫有一定的正向作用, 但对其余 6 种主要害虫成虫的寿命和生殖没有影响 (Liu *et al.*, 2017a)。

近年来, 在中国多个地区相继建造了大批具有人工调控环境能力的永久性现代化玻璃温室用于花卉的生产, 引种培育非本地栽培品种的花卉并实现全年生产供应, 而目前寄生蜂在温室花卉害虫防治过程中的占有重要地位。花卉植物可分成观花植物和观叶植物两大类, 其中观花植物能够提供花粉及花蜜作为寄生蜂的食物或者捕食性天敌的替代食物, 有利于建立天敌群落, 起到了类似于“蜜源植物”的作用, 所以同一温室内栽种花卉种类及配比不同也会影响温室内寄生蜂群落的结构与丰度 (赵紫华等, 2013; 付雪等, 2014)。

**6.2.3 植物支持系统和生态调控** 现代农业的大面积单一化种植改变了原本多物种和谐共存的生态环境, 使得多种虫害频繁发生甚至无法控制。因此, 从增加生物多样性、提高生态系统的稳定性着手的改善生态环境以利于天敌种群增殖或定居, 恢复和提高天敌昆虫的自然控害作用是一直以来指导包括寄生蜂在内的天敌昆虫研究和应用的生态原则 (赵修复, 2003)。随着生物防治基础和应用研究的深入, 植物在保护性生物防治、维持和促进天敌控制害虫中的重要性和作用日益凸显和受到关注, 目前除了蜜源植物, 其他一些功能植物, 如储蓄植物、栖境植物、诱集植物、指示植物、护卫植物等都在支持天敌因生存和繁殖方面发挥了重要的作用 (陈学新等, 2014)。生长在田头、地埂、路边、沟渠、果园内树行间的功能植物为寄生蜂提供了食物、繁殖场所、越冬或夏眠场所等, 改善了寄生蜂生存的微环境, 在作物收获或施药等农事操作干扰时为寄生蜂提供了庇护所, 有利于寄生蜂种群的增长, 维护农业生态系统的平衡, 是保护型生物防治的重要组成部分 (陈学新等, 2014; Zou *et al.*,

2020)。

通过作物生态系统内的植物种类和布局的管理,改善天敌昆虫生存环境,恢复或者提高原有寄生蜂对寄主害虫的控制作用,而合理管理措施的提出是需要以对不同作物系统内生境复合程度对寄生蜂的影响为基础的。在稻田生态系统中,稻田、田埂和毗邻杂草地的天敌昆虫种类和动态差异明显。如广东省四会市大沙镇稻田中褐飞虱卵期寄生蜂群落结构和动态研究表明,共获得 19 种卵寄生蜂,其中稻虱缨小蜂、长管稻虱缨小蜂和拟稻虱缨小蜂是群落中的优势种群,它们对控制褐飞虱卵期的存活率起主要作用,在水稻生长前期、中期和后期,寄生蜂对褐飞虱卵的平均寄生率分别达到 76%、70%和 50% (毛润乾等, 1999, 2000)。如在福建古田稻田及其毗邻杂草地的系统调查发现稻田中有隶属 16 科的 67 种寄生蜂,而毗邻杂草地中有隶属 19 科 96 种寄生蜂 (李志胜等, 2002; 徐敦明等, 2004)。如在江西省万载县国家有机食品 (稻米) 生产基地的有机水稻生产区调查到 2 目 8 科 28 种寄生性昆虫 (梁朝巍, 2011)。分析表明,田埂和稻田周围杂草地的寄生蜂群落的均匀性指数比稻田低,但物种丰度、多样性、优势集中度指数均比稻田高,因此,稻田周围的田埂及杂草地生境是稻田寄生蜂的种库,对稻田寄生蜂群落的重建和种群保存有重要影响。适当保留田埂杂草和稻田周围的杂草地,种植功能植物,增强农业景观的异质性,从而提高寄生蜂的多样性和控害效能 (郑云开等, 2014)。所以,针对稻田飞虱类害虫,首先可以保留具有寄生蜂保育能力的栖境植物,比如能吸引多种飞虱产卵的稗草,越冬期的马唐 *Digitaria sanguinalis* 和牛筋草 *Eleusine indica*, 水稻种植前期的看麦娘 *Alopecurus aequalis* 和李氏禾 *Leersia hexandra*, 然后种植提供替代寄主的储蓄植物,如茭白 (茭白-长绿飞虱-缨小蜂)、秕谷草 *Leersia sayanuka* (秕谷草-伪褐飞虱 *Nilaparvata muii* -稻虱缨小蜂), 再是种植花期较长的蜜源植物 (芝麻、大豆或者莎草类和阔叶类杂草)、诱集植物 (香根草 *Vetiveria zizanioides*) 等, 由此促进水稻生态系统中稻飞

虱卵寄生蜂的大量繁殖,提高稻田附近寄生蜂的数量,降低稻田稻飞虱的种群数量 (张纯青和金行模, 1980; 林拥军等, 2011; 郑许松等, 2013; 朱平阳等, 2015, 2017)。单季晚稻区也可以采用同样的策略。冬季稻田种植绿肥紫云英 *Astragalus sinicus*, 为天敌提供越冬场所及花粉花蜜等食料; 稻田田埂全年保留杂草,尤其是禾本科杂草,为天敌提供替代寄主、猎物、庇护所及越冬场所; 稻田中部分别设置种植茭白和芝麻的区域,作为天敌库繁殖并持续释放稻飞虱卵寄生蜂和为之提供补充营养蜜源; 为了进一步加强效果,田埂种植红花酢酱草、波斯菊 *Cosmos bipinnata*、硫华菊 *Cosmos sulphureus* 等显花植物和撒种显花植物以及在稻区机耕路两边及较宽的田埂上种植诱集植物香根草,利用其对水稻螟虫的诱集效应诱杀螟虫,结果表明,自 2009 年实施以来到 2014 年为止,原有稻田生态功能得到良好修复,稻纵卷叶螟被持续控制在较低的水平,杀虫剂的使用减少了 93.75% (郑许松等, 2017)。

在山东省日照的花生产区,虽然蛭蟥寄生蜂天敌资源比较丰富,但因生存环境的恶化造成种群密度过低所以不能发挥控害作用。研究人员针对性地在花生田周边种植红麻、蓖麻等各种蜜源植物,采取花生与玉米、甘薯、大豆等不同作物间作措施,改善花生田间的生态环境,以保护利用暗黑鳃金龟 *Holotrichia parallela* Motschulsky 的优势寄生性天敌-弧丽金龟钩土蜂 *Tiphia popillivora* Rohwer 的栖息环境。通过多年的连续努力,寄生蜂与蛭蟥的益害比连年增大,最终暗黑鳃金龟幼虫在起始危害期就被有效抑制,目前该花生产区对蛭蟥已不再进行化学防治 (陈红印等, 2003)。

在广州对两种不同生境的荔枝园系统 (林下植被为稀疏的亚热带常见杂草及零星灌木的单一园,近百种亚热带常绿阔叶高大乔木、丛生灌木和繁茂杂草片状混合种植的复合系统) 的寄生蜂群落调查发现,虽然姬小蜂和跳小蜂这两类寄生蜂在两种生境中都占据重要地位,但是复合园中寄生性天敌种类较丰富、数量较多、均匀

性程度高于单一园,但是优势集中度低(刘德广等, 1999)。在辽宁昌图按 5 个非耕作生境比例(0-10%、10%-20%、20%-30%、30%-40%和40%-50%)分别评估不同非耕作生境组成对包括寄生蜂在内的玉米螟天敌数量的影响,发现玉米螟天敌数量随着非耕作生境比例呈先增后减,其中以林地为主或村落、草地为主的非耕作生境的比例为 20%-30%时天敌数量达最大值(边振兴等, 2019)。作为我国棉花重点产区的新疆具有独特的生态环境和光热资源,且农田都是位于荒漠绿洲交界地带,与荒滩、荒山、戈壁、沙漠、沙丘相交错,那么与荒漠、盐碱地等的过渡带以及棉田周边杂草(红柳、盐爪爪等植物)能保有明显多于单一棉田、分属于蚜茧蜂、金小蜂等 14 个科的寄生蜂,所以为棉田寄生蜂提供了丰富的种库资源(武维霞等, 2009)。所有对作物田块周边生境植被组成对寄生蜂保育作用,都为利用合理制定生态调控策略促进寄生蜂的害虫控制功能提供了理论和实践的依据。

## 7 总结和展望

寄生蜂在生物防治过程中的应用研究在过去和现在仍然主要是以针对一种寄生蜂、一种寄主(重大害虫)或者一个作物生态系统开展,个性化的特色很突出。研究内容从早期以分类和资源多样性调查、种群动态调查、生命表组建为主,发展到利用大分子、全基因组、转录组测定技术通过基因、蛋白的鉴定和转录水平变化分析解析寄生蜂生物学、生理学、营养学、繁殖学和生态学的特征以及对寄主的调控作用,为更好地在生物防治中应用寄生蜂并高效的发挥它们的控害作用提供了科学依据、奠定了理论基础,而且也为我国重大农业害虫的可持续控制提供了技术支撑和条件,保障了我国绿色、安全的农业生产。

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