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多寄主型寄生性天敌昆虫的寄主适应性及其影响因素

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摘要:寄生性天敌昆虫对不同寄主资源的适应能力是其存活和繁殖的必要条件,它们的寄主选择行为则是其重要的适应结果。多寄主型寄生性天敌昆虫虽然对某种特定寄主资源的利用效率可能不如单寄主型寄生蜂,但却有利于拓展更宽的寄主范围,因此对环境的适应能力更强,更容易在自然界维持其种群的生存。统计结果也表明多寄主型天敌的生物防治效果往往比专食性天敌更高。有时生物防治成功的关键可能并不在于所利用的天敌种类的不同,而在于天敌的不同生物型或地理宗。总结了多寄主型寄生性天敌昆虫的寄主适应能力及其影响因素。寄生性天敌昆虫不仅因地理隔离产生种群分化,也可能因寄生不同的寄主产生种群内的分化,从而更加适应寄主的生活特性和栖境条件。寄主种类、寄主发育阶段、寄主大小、寄主营养、寄主免疫反应、寄主逃避反应、其它天敌的竞争、寄主共生或共栖生物的存在、寄主植物、天敌自身的学习能力及其共生微生物等多种因素对寄生性天敌昆虫的寄主适应性可产生影响。展望了多寄主型寄生性天敌昆虫对新寄主资源的拓展利用能力和适应性在生产上的可能应用前景和途径,以期为明确天敌与寄主间的互作关系,人工驯化寄生性天敌昆虫增强对靶标害虫的控制作用,合理利用天敌提高生物防治效率提供新的思路和理论支持。

关键词:多寄主型寄生性天敌昆虫;寄主适应;进化;寄主相关的种群分化;生物防治

Host adaptations of the generalist parasitoids and some factors influencing the choice of hosts

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Abstract: Adaptations of parasitoids to fluctuating host resources are essential for their survival and reproduction. Among these adaptations, host selection behaviors have important consequences for adapting to an ever changing environment. Generalists parasitoids are perhaps less efficient at discovering and using one particular host resource compared to specialists, but they have the advantage of exploiting a wider range of host resources. When one host population is at low density, generalist parasitoids have ability to maintain a relative high population density on other hosts. The effectiveness of biological control statistically tends to be higher when the agents used are generalists than when they are specialists. Sometimes the key to successful biological control may not lie in discovering another species, but instead may rely on the use of different biotypes or geographic races of biocontrol agent. The present paper summarizes the host adaptations of generalist parasitoids and some factors influencing the choice of hosts. Parasitoids will differentiate among populations of themselves not only due to geographic isolates, but also duo to different hosts they parasitized for better adaptations to some particular attributes of hosts' life and the microhabitats therein. The selection by parasitoids of which species to use as hosts is influenced by multiple factors such as host species, host developmental stages, host sizes, host nutrition, host immunoreactions, host escape responses, competition from other natural enemies, presences of host associated symbionts or mutualists, host plants, learning behaviors of parasitoids, and symbiotic microorganisms of parasitoids, etc. In addition, the potential utilization of novel host resources, the mechanisms of exploitation, and host adaptations of generalist

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parasitoids are discussed. This discussion may provide new ideas and theoretical support for improving biological control efficiency by enhancing our understanding on host-parasitoid interactions and artificially selecting for novel parasitoid/host relationships for augmenting the management of target insect pests.

Key Words: generalist parasitoids; host adaptation; evolution; host-associated differentiation; biological control

多寄主型寄生性天敌昆虫是指能寄生两种以上寄主的寄生性天敌,也称多食性天敌。寄主专化性强通常被认为是优秀天敌昆虫所应具备的主要特征之一[1]。然而据统计,多寄主型天敌的生物防治效果往往比专食性的天敌更高[2]。专食性寄生蜂在寄主不致中断的环境中容易提高寄生率,但对于寄主发生期易脱节的种类,寄生率却难以维持在较高水平。而多寄主型的寄生性天敌昆虫虽然在自然界容易维持生存,但因寄主分散,对某一特定害虫的寄生率不易提高[3]。那些虽然可寄生多种寄主,但主要集中于某些生活特性相近的种类,如某一科的昆虫,特别是在多种寄主共存的环境中对某些种类具有选择嗜好性的寄生者在生物防治上可能具有更好的应用前景。寄生性天敌昆虫的专化性可以是栖境层次,也可以是寄主层次的,这两种类型的寄生物生存策略有所不同。多寄主型天敌对某种特定资源的利用效率可能不如专食者,但有利于拓展更宽范围的寄主资源。而且嗜好性并不总是与寄主适合性相关,如栖境专一的缢管蚜茧蜂 *Aphidius rhopalosiphi* 对处于相同环境下的不同寄主表现出相似的反应,而多寄主型的无网长管蚜茧蜂 *A. ervi* 则表现出明显的寄主选择嗜好[4]。多寄主型的豆象金小蜂 *Dinarmus basalis* 能识别寄主的质量,在较差的寄主上偏向于产生雄性后代[5]。

目前在应用害虫天敌进行生物防治的实践中,多利用替代寄主人工繁殖,然后在野外释放,这样有可能会造成控制效果不理想的情况发生。天敌对寄主害虫的搜索、发现和攻击能力以及对目标害虫的适应性和喜好程度是影响生物防治效果的重要因素。因此,研究天敌因寄主不同可能产生的种群分化及其寄主适应性,对于充分利用天敌昆虫,提高生物防治的效率十分关键。本文对多寄主型寄生性天敌昆虫的寄主适应性及其影响因素进行了总结,以期为生产上合理利用寄生性天敌昆虫开展害虫生物防治提供帮助。

1 寄主相关的种群分化

昆虫种群在进化过程中为适应寄主和环境的变化常常分化为不同的寄主专化型(或称生物型、寄主宗),在植食性昆虫中相关的研究报道已经较多,特别是多食性昆虫[6-9]。不同的寄主专化型对特定的寄主产生取食偏好,甚至强烈的依赖,如油菜上的桃蚜不能在桃树上存活[10],黄瓜上的棉蚜不能在棉花上建立种群,棉花上的棉蚜也不能在黄瓜上建立种群[7]。不同寄主专化型的昆虫不仅在遗传上存在差异[11],有些在形态和生态习性上也有所不同[12-13]。多食性的昆虫需要在代谢上适应多种不同的寄主化学物质而付出更大代价,因而促使昆虫向专食性方向进化,减少种内竞争、合理分配资源,将更多的能量投入到种群的繁殖上,提高其生态适应性[14]。有人认为这是同域物种形成的关键步骤[15]。研究表明,气温是影响植食性昆虫专化性的形成及其程度的重要因素,如热带地区鳞翅目幼虫取食的植物种类比温带地区更专一[16]。

关于寄生性天敌昆虫种群分化的研究目前还不多见。事实上,植食性昆虫因取食植物不同产生的分化也可能导致寄生蜂种群为适应寄主栖境的变化而发生相应的分化[17]。Perez-Maluf 等[18]认为寄生蜂对寄主栖境的反应可产生自然分化,形成不同基因型的种群。Cônsoli 等[19]报道了短翅姬小蜂 *Melittobia digitata* 为适应新寄主资源和栖境移殖而分化为长翅型和短翅型 2 种生物型。寄生几种果蝇 *Drosophila* spp. 的棒足环腹瘿蜂 *Leptopilina clavipes* 在欧洲南部和北部之间产生了种群分化,南欧品系接受所有供试寄主,而欧洲西北部品系的寄主专化性增强了[20]。大螟盘绒茧蜂 *Cotesia sesamiae* 在肯尼亚存在 2 种生物型[21],无毒型由于寄主玉米干夜蛾 *Busseola fusca* 血淋巴的免疫反应而不能完成发育,具毒型则能够通过毒液中的一种特殊蛋白克服寄主的免疫系统[22]。有些寄生蜂的不同生物型可能利用不同的线索识别和标记寄主,这种行为上的差异必然会导致种群间基因流动性的降低,分化加剧[23]。

引进天敌到新地区防治入侵害虫的成功率往往较低,一个可能的解释是天敌不能适应新地区的气候条件。Phillips 等[24]通过人为定向选育适应引进地气候条件的寄生蜂生物型大大提高了防治成功率,这在入侵害虫的传统生物防治实践上是很有意义的。但还有一个可能性是天敌对入侵地的寄主害虫不适应,因为入侵地的害虫可能为了适应当地的生态环境已经分化为不同的生物型或地理宗了。Kenis 等[25]研究表明,欧洲木蠹象茧蜂 *Eubazus semirugosus* 的山区生物型由于滞育特性比低地生物型更加适合北美地区的白松木蠹象 *Pissodes strobi* 的生活习性,最适于引入加拿大而成为控制该害虫的有力天敌。寄生琉璃叶蝉 *Homalodisca coagulata* 的叶蝉卵柄翅缨小蜂 *Gonatocerus ashmeadi* 在不同的地理品系之间存在显著的遗传分化[26],这在生物防治应用上是有价值的。生物防治成功的关键有时可能不在于所利用的天敌种类的不同,而在于天敌的不同地理宗或生物型。Ruberson 等[27]发现墨西哥生物型的马铃薯甲虫卵姬小蜂 *Edovum puttleri* 比哥伦比亚生物型更耐低温,且 2 种生物型对农药的敏感性不同,寿命、对寄主卵的利用、净生殖率、后代性比等方面也有差异。野生栖境和农作物栖境下的粉蝶盘绒茧蜂 *Cotesia glomerata* 存在行为上的遗传分化[28]。Vaughn & Antolin[29]报道菜少脉蚜茧蜂 *Diaeretiella rapae* 因利用的寄主不同而产生了种群内遗传结构上的分化,以更加适应寄主的栖境条件。但也有一些相反的报道,如 Baer 等[30]认为菜少脉蚜茧蜂不存在寄主相关的遗传分化。Cronin & Abrahamson[31]发现广肩小蜂 *Eurytoma gigantea* 虽然对不同植物种类上的寄主瘿实蝇 *Eurosta solidaginis* 在适合度上存在一定差异,但并没有随着寄主分化而产生相应的寄主宗。Althoff[32]指出寄生丝兰蛾 *Prodoxus* spp. 的长角旋小蜂 *Eusandalum* sp. 的遗传分化与种群间的地理距离相关,不太可能是因寄主或寄主植物不同而引起的。因此,关于寄生蜂种群分化的机制还有待深入研究。

2　寄生性天敌昆虫寄主适应的影响因素

寄生性天敌昆虫的寄主专化性和寄主选择与寄主对寄生物发育的适合性相关。寄生性天敌昆虫的寄主搜索行为不仅使其成功选择了多数适合发育的寄主,而且在形成其寄主范围上具有重要作用[33]。寄生性天敌昆虫的寄主范围可能是由影响寄主适应性的特性或者是由影响它们觅食行为的特性所决定的,或由二者共同决定的[34]。生物对物质和能量的利用效率意味着适应程度的高低,任何能够增进生物个体对环境物质利用率的特征即为适应,能利用其他个体不能利用的物质资源和能量的个体就是最适者[35]。如寄生蜂调整其产卵计划是对寄主资源变化的一种有效适应[36]。当可利用的寄主质量存在差异时,寄生蜂的寄主选择行为是其重要的适应结果。储备能源物质如脂类化合物,可减少未来当食物不足时可能导致的不利影响。有些寄生蜂种类的成虫没有脂肪生成机制,这就可能会迫使寄生蜂通过开发新的寄主资源解决食源短缺问题[37]。

寄生性天敌昆虫的寄主适应性是一个非常复杂的问题,不仅涉及到它们是多寄主型还是寄主专化型的,而且还与食性专化的程度有关。寄主种类、寄主的发育阶段、寄主的个体大小、寄主的营养、寄主的免疫反应、寄主的逃避反应、其他天敌的竞争、寄主共生或共栖生物的存在、寄主取食或栖息的植物种类、天敌自身的学习行为、天敌的共生微生物、环境温度等诸多因素影响到寄生性天敌昆虫的寄主适应性。在寄生蜂的寄主定位活动中,行为生态的适合先于生理和生化的适合。很多时候非自然寄主的生理生化条件适合寄生蜂的生长发育,但却因为行为或生态上的局限使得非自然寄主不能或不会被寄生蜂寄生[38]。Morehead 和 Feener[39]认为寄主定位和寄主接受行为是决定天敌寄主专化性的主要原因,如经测定蚁蚤寄蝇 *Apocephalus paraponerae* 潜在的寄主范围比实际的要大得多。寄生性天敌昆虫接受寄主后,寄主的适合性也是限制其仅适应某些寄主种类的因素[3]。

2.1　寄主种类

寄主种类对寄生蜂后代的适应性影响最大,因此寄生蜂雌成虫的终极目标是寻找到最适合后代发育的寄主资源。很多寄生蜂是通过来源于寄主或与寄主相关的化学气味物质寻找和识别寄主害虫的。头甲肿腿蜂 *Cephalonomia tarsalis* 主要是利用寄主体表的化学气味和与寄主接触后寄主的活动来识别寄主[40]。寄生咖啡果小蠹 *Hypothenemus hampei* 的咖啡小蠹肿腿蜂 *Prorops nasuta* 的寄主搜索行为是由寄主与受害植物复合体的化学气味所诱导的[41]。专化性的果蝇环腹瘿蜂 *Leptopilina boulardi* 不仅对寄主产生趋性反应,对可释放相同

化学气味的一些非寄主种类也产生趋性反应[42]。

昆虫能够非常快速地进化以适应变化的环境[43-44],有些寄生蜂对寄主资源的适应也是如此。Cassanello 等[45]发现亚洲玉米螟赤眼蜂 *Trichogramma ostriniae* 能寄生多种鳞翅目昆虫的卵。寄生椰树黑头织蛾 *Opisina arenosella* 幼虫的云斑棱角肿腿蜂 *Goniozus nephantidis* 还可用大蜡螟 *Galleria mellonella* 和米蛾 *Corcyra cephalonica* 幼虫成功进行饲养[46]。在非选择性条件下,川硬皮肿腿蜂 *Sclerodermus sichuanensis* 能寄生多种非自然寄主的昆虫种类[47]。寄生白蜡窄吉丁 *Agrilus planipennis* 的白蜡吉丁肿腿蜂 *Sclerodermus pupariae* 还能取食和寄生柑桔窄吉丁 *Agrilus auriventris*、苹小吉丁 *A. mali*、花椒窄吉丁 *A. zanthoxylumi*、核桃脊胸纹吉丁 *Nalanda* sp.、咖啡脊虎天牛 *Xylotrechus grayii*、复纹狭天牛 *Stenhomalus complicatus*、光肩星天牛 *Anoplophora glabripennis*、栗山天牛 *Massicus raddei*、松褐天牛 *Monochamus alternatus*、麻天牛 *Thyestilla gebleri* 等多种吉丁甲和天牛的幼虫,且后代能正常完成生长发育[48]。棉铃虫 *Helicoverpa armigera* 完全适合作为红足侧沟茧蜂 *Microplitis croceipes* 室内人工繁育的替代寄主,与其自然寄主谷实夜蛾 *Helicoverpa zea* 和烟芽夜蛾 *H. virescens* 一样[49]。

用非自然寄主豌豆蚜 *Acyrthosiphon pisum* 连续饲养数代后的微毛蚜茧蜂 *Aphidius microlophii* 寄生率显著提高[50]。室内用米象 *Sitophilus oryzae* 连续繁殖的象虫金小蜂 *Anisopteromalus calandrae* 和米象娜金小蜂 *Lariophagus distinguendus* 在换用绿豆象 *Callosobruchus chinensis* 饲养后,2 种寄生蜂的功能反应和数值反应减弱,攻击率明显下降,寿命缩短[51]。象虫金小蜂至少需要经历 2 个世代适应非自然寄主绿豆象,但一旦适应新寄主后,其搜索效率趋于稳定[52]。一种新害虫的传入可能引起寄生蜂寄主嗜好性的快速改变,在日本北海道,粉蝶盘绒茧蜂 *Cotesia glomerata* 原本寄生菜粉蝶 *Pieris rapae* 幼虫,当欧洲粉蝶 *P. brassicae* 入侵后,粉蝶盘绒茧蜂对菜粉蝶的寄生作用明显降低,而对欧洲粉蝶的寄生率上升。寄生粉蝶盘绒茧蜂的 2 种重寄生蜂也相应地产生了分化,蛹期重寄生蜂毛虫灿金小蜂 *Trichomalopsis apanteroctena* 逐渐转移到了寄生欧洲粉蝶的盘绒茧蜂上,而幼虫期的重寄生蜂弯沟啮小蜂 *Baryscapus galactopus* 则仍然保持寄生菜粉蝶的茧蜂[53]。欧洲粉蝶的入侵在短时间内就改变了粉蝶盘绒茧蜂及其蛹期重寄生蜂毛虫灿金小蜂的寄主利用习性,这种寄主选择的变化可能是由于寄生蜂对 2 种类型寄主的适合性差异所引起的。

用非自然寄主饲养的寄生蜂有时存在活力降低的现象,即使表面上看寄生蜂似乎没有受到任何影响[54]。寄主种类、寄主食料对前裂长管茧蜂 *Diachasmimorpha longicaudata* 后代的寿命、大小和繁殖力具有明显影响[55]。柯氏蚜茧蜂 *Aphidius colemani* 在不同种类蚜虫寄主之间的平均寄生率、后代存活率、发育历期和成蜂体重具有显著差异[56]。用欧洲玉米螟 *Ostrinia nubilalis* 卵连续饲养的甘蓝夜蛾赤眼蜂 *Trichogramma brassicae* 比用地中海粉斑螟 *Ephestia kuehniella* 卵连续饲养的种群能更好地接受其自然寄主欧洲玉米螟卵。在利用替代寄主大量繁殖赤眼蜂时,寄生蜂对靶标害虫的接受和适合性是重要的质量评价指标[57]。Takada 等[58]曾报道松毛虫赤眼蜂 *Trichogramma dendrolimi* 虽然经过人工寄主地中海粉斑螟卵连续繁殖 12 代之后,它对其自然寄主甘蓝夜蛾 *Mamestra brassicae* 卵的选择嗜好性仍然未丧失,对甘蓝夜蛾卵的寄生率是地中海粉斑螟卵的 2 倍。异色瓢虫 *Harmonia axyridis* 在用替代寄主地中海粉斑螟卵连续饲养 100 多代以后对蚜虫的敏感性下降。由于长期没有接触猎物的气味刺激,这种用人工饲料繁殖的天敌释放后要比用自然猎物饲养的个体经历更长时间和遭遇猎物更多次数,才能学会捕食目标害虫[59]。二星瓢虫 *Adalia bipunctata* 当分别用豌豆蚜 *Acyrthosiphon pisum* 和黑豆蚜 *Aphis fabae* 连续单独饲养 6 代后,它们对这 2 种蚜虫的选择性和适合性(存活率、繁殖力、体重、寿命)均明显提高,发育历期和产卵前期缩短,而对其他猎物的捕食嗜好性显著降低[60]。寄生蜂对一种新环境(如食料、寄主和温度)的适应,很可能要以降低对原先环境的适合度为代价[61]。因此,寄生蜂必须对在自然寄主和新拓展的寄主上保持高适合度的能力进行权衡,这说明寄主利用的遗传基础可能限制了寄生蜂寄主范围的扩大[62]。这些研究结果表明多寄主型寄生性天敌昆虫的生活史策略对开发新的食物资源是有利的,因此可以通过室内的人工驯化,使其对目标害虫具有更强的嗜好性。但问题是如果利用替代寄主或人工饲料繁殖天敌,则可能降低对自然寄主的搜索能力和攻击能力。

2.2　寄主发育阶段

很多寄生蜂对寄主的不同龄期也有明显的选择性。如中红侧沟茧蜂 *Microplitis mediator* 最偏好寄生甘蓝夜蛾 *Mamestra brassicae* 的 1 龄幼虫[63]。桨角蚜小蜂 *Eretmocerus mundus* 偏好寄生 2—3 龄的烟粉虱若虫[64]。白蜡吉丁柄腹茧蜂 *Spathius agrili* 仅寄生 3—4 龄寄主幼虫[65]。白星海芋恩蚜小蜂 *Encarsia inaron* 对不同龄期的寄主温室白粉虱 *Trialeurodes vaporariorum* 的寄生率显著不同[66]。双斑截尾寄蝇 *Nemorilla maculosa* 对寄主草地螟 *Loxostege sticticalis* 幼虫的龄期和身体部位具有明显的选择性[67]。理论模型预测寄生蜂的产卵决策将选择最适于寄生蜂后代发育的寄主。大多数寄生蜂已经在利用寄主某一特定的发育阶段方面进化为物种的适应性,但有些寄生蜂也能够选择多个发育阶段的寄主进行产卵,如一种重寄生的食蚜蝇跳小蜂 *Syrphophagus aphidivorus* 既能寄生活体马铃薯长管蚜 *Macrosiphum euphorbiae* 体内的黑蚜茧蜂 *Aphidius nigripes* 幼虫,也能寄生僵蚜内的蚜茧蜂蛹[68]。这类寄生蜂的寄主适应能力必然更强。

2.3　寄主个体大小

寄主个体大小和体壁厚薄等均对寄生性天敌昆虫后代的发育有影响。寄主太大,体液过多,容易腐烂变质;寄主太小,营养不足;寄主体壁太厚,寄生蜂后代不能成功羽化[3]。寄主个体大小对大螟盘绒茧蜂 *Cotesia sesamiae* 的发育和繁殖潜能具有显著影响[69]。粉蝶盘绒茧蜂 *C. glomerata* 每窝产卵量的适应性与寄主的个体大小和相遇概率有关[70]。蒋学建和周祖基[71]报道寄主体壁硬度越小,越容易被川硬皮肿腿蜂寄生成功。

2.4　寄主营养

当可利用的寄主质量存在差异时,寄生蜂的寄主选择行为是其重要的适应结果。在植食性昆虫中的确发现某些不同的寄主专化型之间营养需求不同,如取食不同水稻品种的褐飞虱 *Nilaparvata lugens* 寄主种群对食料中氨基酸的需求存在明显分化[72]。有关寄生蜂不同生物型对营养需求的差异鲜见报道,但寄主质量对寄生蜂后代适合性的影响较大。而且有研究表明寄生蜂的寄生在一定程度上可改变寄主的生理状况和营养价值,从而提高和改善寄生蜂后代的生长发育。丽蝇蛹集金小蜂 *Nasonia vitripennis* 的生殖力和发育依赖于寄主质量,后代分配和性比也是根据寄主质量进行调节的。寄主的生理和营养状况影响寄生蜂的产卵行为和生长发育,寄生蜂在不同营养条件的寄主上的发育时间和成虫个体大小存在明显差异[73]。川硬皮肿腿蜂寄生替代寄主后,在一定时间内寄主机体蛋白、糖类、氨基酸等成分的含量,蛋白水解酶、淀粉酶及海藻糖酶的活力发生了显著变化[74]。虫体肌肉组织、脂肪组织以及消化道、马氏管、气管等组织结构也产生了明显改变[75]。这可能是寄生蜂毒液产生的作用。蚜虫中的胚胎生殖完全依靠内共生细菌(主要是 *Buchnera*)的功能,被无网长管蚜茧蜂寄生的豌豆蚜 *Acyrthosiphon pisum* 比未寄生的蚜虫具有更多较高生物量的带菌细胞(mycetocytes)和较低生物量的胚胎生殖,表明容性内寄生蜂的生长发育从蚜虫的胚胎生殖中分流出了部分营养[76]。无网长管蚜茧蜂的寄生改变了寄主豌豆蚜的生理和代谢方向,使其更有利于寄生蜂幼体的生长发育。被无网长管蚜茧蜂寄生的豌豆蚜体内合成了 2 种丰富的特异蛋白,是寄生蜂后代幼体生长发育的重要营养来源[77]。被寄生蚜虫体内自由氨基酸的总量也显著升高,特别是酪氨酸的含量比未寄生蚜虫上升了 4 倍[78]。当寄主质量变化时,最适觅食理论认为寄生蜂是以提高个体适应性来选择寄主的。但容性寄生蜂的寄主选择似乎并不能反映当时的寄主质量,而可能是根据对寄主幼虫未来的生长发育和资源可利用性做出的寄主选择[79],因为被容性寄生蜂寄生后的寄主仍然要继续存活一段时间,这对寄生蜂后代的成功发育是必需的。此外,寄主适合性还会受到被寄生寄主随后的取食率和食料质量的强烈影响[80]。寄生蜂的成功繁殖依赖于雌蜂对寄主是否适合于后代幼虫的发育进行精确评估的能力。但实际上寄生蜂在接受寄主之前对寄主也未必都进行过充分的评估,因而有时也会选择质量较差的寄主产卵。多寄主型的容性无网长管蚜茧蜂在寄主土豆沟无网蚜 *Aulacorthum solani* 的 2 龄若虫上繁殖最成功,而 3 龄和 4 龄若虫上的繁殖性能则下降。然而当给予雌蜂选择寄主产卵时,成蜂却偏好寄生老龄蚜虫,不管其后代发育的寄主适合性是否降低[81]。

2.5　寄主的免疫反应和逃避反应

寄主昆虫的免疫反应影响寄生蜂的生理寄主范围,尤其是对于容性内寄生蜂。不同种类的寄生蜂在寄生

寄主后不同的时间可能利用不同的策略应对寄主的免疫反应[82]。寄主的反抗是蚜茧蜂产卵行为进化的重要原动力[83]。陈倩等[84]报道通过低温贮存可降低替代寄主的活动和反抗能力,提高哈氏肿腿蜂 *Sclerodermus harmandi*(即管氏肿腿蜂 *S. guani*)[85]的人工繁殖效率。缩基无臂茧蜂 *Asobara tabida* 的寄主选择行为与寄主黑腹果蝇 *Drosophila melanogaster* 的逃避能力平行进化,只要给予合适的选择压力,寄生蜂的寄主选择行为能够快速进化以适应迅速变化的环境[44]。捕食者对蚜虫的攻击和捕食偏好性受到寄主行为和化学防御对策的影响,还受到猎物适口性和猎物营养价值的影响。猎物从植物上获得的有毒或致敏化学物质是决定捕食者嗜好性的重要因子[86]。

2.6 其他天敌的竞争

来自寄生蜂种内或种间其他天敌的竞争也会影响到寄生蜂对寄主的选择利用。寄生蜂之间的竞争是造成缩基无臂茧蜂不同地理宗在生活史选择上产生差异的原因之一[87]。寄生蜂产于某寄主上的后代性比还受到其它雌蜂在该寄主上产卵量的影响[88-89]。很多寄生蜂能够感知其他寄生蜂的寄主标记信息素,从而避免重复寄生。有些寄生蜂遇到已寄生的寄主后,先杀死前一寄生蜂留下的后代再产下自己的卵,从而避免其后代在资源上的竞争[90]。寄生蜂的存在对食蚜蝇的寄主选择行为也有影响[91]。

2.7 寄主共生或共栖生物的存在

某些与寄主共生或共栖的生物对天敌昆虫的寄主适应性产生影响,有些影响对天敌是不利的,而另一些影响是有益的。蚂蚁的保护是促进蚜茧蜂产卵行为进化的原动力[83]。研究表明,有懒弓背蚁 *Camponotus brutus* 或斑腹脊红蚁 *Myrmicaria opaciventris* 保护的皱龟蝽 *Caternaultiella rugosa* 卵块被卵跳小蜂 *Ooencyrtus* sp. 寄生的概率显著低于没有蚂蚁保护的卵块[92]。蚂蚁的存在也是影响食蚜蝇选择猎物的主要因素之一[91]。

具有内共生细菌沙雷氏菌 *Serratia symbiotica* 或 *Hamiltonella defensa* 的豌豆蚜 *Acyrthosiphon pisum* 对无网长管蚜茧蜂 *Aphidius ervi* 攻击的抵抗能力增强[93-94],而同时带有这 2 种共生菌的豌豆蚜比仅具其中 1 种共生菌的抗性又更强[95]。温度显著影响到带共生菌的豌豆蚜对无网长管蚜茧蜂攻击的抵抗力,在一定范围内,环境温度越低,蚜虫对寄生蜂的抗性越强[96]。

而一些寄主害虫的外共生菌类则可能给寄生蜂带来好处。有些寄生蜂对与寄主伴生的微生物的气味产生了适应,常常通过这类化学线索搜索并发现寄主,特别是对于一些隐蔽性强的蛀干害虫。如黑色枝跗瘿蜂 *Ibalia leucospoides* 对寄主云杉蓝树蜂 *Sirex noctilio* 的共生真菌淀粉韧革菌 *Amylostereum areolatum* 产生趋性反应,不论是松木上自然生长的还是人工培养的真菌气味均对寄生蜂有吸引作用[97]。寄生树蜂幼虫的黑色皱背姬蜂 *Rhyssa persuasoria* 对伴生于寄主蛀道内的淀粉韧革菌也具有强烈的趋性反应[98-99]。木小蠹长尾金小蜂 *Roptrocerus xylophagorum* 和苍白柄腹茧蜂 *Spathius pallidus* 可被带有寄主害虫并感染了线嘴壳属 *Ophiostoma* 蓝变菌的火炬松树皮或木段的气味所吸引[100],表明寄主蛀道内的共生菌有助于寄生蜂寻找寄主。

2.8 寄主植物

害虫取食的植物可直接或间接地影响到害虫天敌的行为。深入了解植物-害虫-天敌系统的协同进化,对于天敌和植物抗虫性的结合利用是有价值的[101]。寄主取食或栖息的植物种类对有些寄生蜂的寄主选择行为可产生显著的影响[102-103],有些寄生蜂甚至对寄主危害的树种具有专化性[104]。前裂长管茧蜂 *Diachasmimorpha longicaudata* 在室内用面粉饲料饲养的寄主桔小实蝇 *Bactrocera dorsalis* 幼虫连续繁殖 160 多代后,对取食番木瓜果实的桔小实蝇幼虫的选择性明显降低。表明即使是同一种寄主,寄主取食的食物不同也会影响到寄生蜂的选择性[105]。

寄主植物的种类强烈影响寄生蜂的生态习性,寄生蜂的适应性可能受到各种能够促进种群表型分化的植物特性的影响。多寄主型寄生性天敌昆虫受到植物特性(如植物的防御性)的影响可能更大[106]。Khan 等[107]发现在玉米或高梁地间作玉米干夜蛾 *Busseola fusca* 和斑禾草螟 *Chilo partellus* 的非寄主植物糖蜜草 *Melinis minutiflora* 可降低作物的受害程度,这是因为糖蜜草的挥发物对这两种害虫具有驱避作用,同时又能招引大螟盘绒茧蜂 *Cotesia sesamiae* 寄生它们,提高天敌的寄生率。甚至不同的害虫取食同一种植物可诱使植

物产生不同的挥发物，招引不同种类的寄生蜂，特别是专化性强的寄生蜂能够识别植物挥发物是否为来自其寄主害虫取食后所产生的。如黑头折脉茧蜂 *Cardiochiles nigriceps* 能够从烟芽夜蛾 *Heliothis virescens* 和谷实夜蛾 *Helicoverpa zea* 取食诱导植物产生的挥发物中识别出其寄主烟芽夜蛾的存在[108]。对不同环境的适应可能是种群发生遗传分化的动力源泉。腰带长体茧蜂 *Macrocentrus cingulum* 对艾蒿上越冬代欧洲玉米螟 *Ostrinia nubilalis* 的寄生率高达 50%，而对同期玉米上正处于滞育状态的玉米螟却不寄生。欧洲玉米螟可能通过寄主转移逃避捕食者、竞争者和寄生物的不利影响[109]。秋麒麟草实蝇 *Eurosta solidaginis* 转移到新的寄主植物上分化为不同的寄主生物型之后，原来的天敌钝腹广肩小蜂 *Eurytoma obtusiventris* 的寄生率显著降低[110]。这从另一个角度说明植食性昆虫可能因为逃避天敌而导致其扩大了寄主植物范围。有些被寄生的寄主幼虫可取食更多能合成对寄生蜂有害的植物化学成分，从而逐渐改变其偏好取食的植物种类[111]。

即使是广食性的捕食性天敌昆虫也会对猎物种类进行选择。如蚜虫取食的植物种类影响食蚜蝇选择其猎物种类[91]。烟草天蛾 *Manduca sexta* 幼虫取食的植物化学成分对捕食者斑腹刺益蝽 *Podisus maculiventris* 的消化率和生长率均产生一定的影响，而且影响大小与环境温度密切相关[112]。

2.9　寄生性天敌昆虫的学习行为

寄生蜂的联系性学习行为是对那些具有隐蔽性和逃避反应的寄主的有效适应。学习行为和接触经验对寄生性天敌昆虫寻找寄主和选择寄主龄期具有明显的影响[113]。植物化学线索因寄生蜂羽化时所经历的环境刺激在决定多寄主型的柯氏蚜茧蜂初始寄主选择时具有重要作用，但学习行为，包括产卵期间经历的线索或与寄主接触等过程，能够修正寄生蜂的初始选择[114]。蝇蛹金小蜂 *Pachycrepoideus vindemiae* 对接受其出生寄主花费的时间明显要少。学习能力和出生寄主的大小对于决定金小蜂攻击率、交配成功、寄主选择和性别分配行为等寄生蜂适应性的关键指标具有重要作用[115]。寄生蜂的学习行为是一个较新的研究领域，国内李保平和刘小宁[116]、李欣和刘树生[117]、杨伟等[118]相继开展过学习对寄生蜂寻找寄主和接受寄主的影响研究。早期的研究一般认为多寄主型寄生性天敌昆虫的学习能力更强，事实上许多食性高度专化的寄生性昆虫也表现出很强的学习能力，特别是那些寄主昆虫能取食较多植物种类的寄生蜂[119]。有些寄生蜂甚至可对与寄主毫无关系的新颖气味产生学习能力，雌蜂经历后表现出明显的嗜好性[120-121]。寄生蜂成虫之前的经历对成虫行为基本没有直接影响，成虫早期所经历的条件羽化作用可显著影响成蜂的寄主搜索和选择行为。成蜂正常羽化后的经历对其行为反应也可产生明显影响，且往往作用更强[117, 119]。据分析，理论上由于幼虫寄生蜂在搜索寄主的过程中需要感受的信息类别多、变异大，需要决策的步骤也较多，因此学习能力最强，尤其是对植物气味的学习，蛹寄生蜂次之，卵寄生蜂相对最弱[119]。寄生蜂的学习行为在生产上可用于人工驯化寄生蜂对靶标害虫及其生活环境的适应性。川硬皮肿腿蜂羽化期和成虫初期经历松枝皮、松针、松节油、杉枝皮等挥发物后，雌蜂对这些植物材料的选择性明显提高[118]。通过驯化后的川硬皮肿腿蜂可适应松褐天牛的生活环境，提高对马尾松上松褐天牛幼虫的寄生能力[122]。但是寄生蜂通过学习所获得的记忆信息只能在当代持续一定的时间，对后代的适应能力没有帮助[123]。因此，深入利用寄生蜂的学习行为，培养天敌对目标害虫的适应性，为害虫生物防治服务。

2.10　寄生性天敌昆虫的共生微生物

某些共生性微生物对寄生蜂和寄主的协同进化具有重大影响。多分 DNA 病毒（PDVs）是膜翅目姬蜂科和茧蜂科寄生蜂体内发现的一类独特的共生性病毒，在寄生蜂产卵时注入到寄主体内，参与寄主的生理调控过程，如抑制寄主免疫系统、调节寄主生长发育、调控寄生蜂与寄主之间的关系等[124-126]。PDVs 具有共生物和病原体的双重功能，与寄生蜂之间存在互惠共生关系，在寄生蜂的成功寄生过程中起着不可替代的作用，是病毒、寄生蜂和寄主昆虫长期相互适应和进化的结果[127]。

Wolbachia 是另一类非常普遍的节肢动物生殖系统中的内共生细菌，是影响宿主性比、群居性和物种形成的重要因素[128]。*Wolbachia* 通过卵的细胞质传播并参与宿主种群生殖活动中的多种遗传调控。*Wolbachia* 能够影响宿主寿命、繁殖力、生育力以及寄主-寄生蜂相互关系[129]，如 *Wolbachia* 的存在对缩基无臂茧蜂的卵子

发生是必须的[130]。*Wolbachia* 既可能在害虫中存在,也可能存在于寄生蜂体内。

3 结语

适应可分为生态适应和进化适应,生态适应是指对当前环境的现实适应能力,更多的与个体在现实环境中的存活能力有关,主要表现为生态幅的宽窄和生理耐受能力的高低等。进化适应是指有机体对过去环境适应的历史积累和对未知环境变化的潜在适应能力。对进化意义上的适应来说,繁殖成功是衡量生物适应好坏的标准,生存则是第二位的[35]。生活习性变异可能是基于遗传特性,或者是由于环境对显性基因的影响所致。缩基无臂茧蜂在调配自身寿命和产卵量之间具有一定的可塑性。食物短缺时减少产卵量,食物充足时提高产卵量。寄生蜂体内储存的脂肪在这种分配过程中起着重要的生理作用,脂肪可用于生殖和存活,这种分配中可塑性的差异因此被认为是产卵量在时间分配上的差异[87]。

生态学是指导生物防治的理论基础[1]。探索寄生蜂对新寄主资源的适应机制,明确天敌与寄主间的互作关系,将为人工驯化寄生性天敌昆虫增强对靶标害虫的控制作用,进一步提高天敌的生物防治效能提供新的思路和理论支持。对于某些重要的害虫种类,可以考虑进行天敌的人工定向选育,培养天敌对目标害虫的取食嗜好性和攻击能力,使驯化的天敌迅速适应目标害虫。在采用传统生物防治策略输引天敌控制外来入侵害虫时,有目标地选择地理条件、气候条件、寄主植物等相似生境中的天敌种类或生物型,可以提高生物防治计划成功的概率。实验室利用替代寄主人工繁殖的天敌在田间或林间释放前,需要对其进行寄主嗜好性研究,以提高天敌对靶标害虫的防治效率。

适应是生物界普遍存在的自然现象和规律,所有生物既要适应其生活的物理环境,也要适应生物环境,才可能得以生存和有效繁衍后代。目前对于寄生性天敌昆虫的寄主适应性机制方面的研究还有许多方面需要深入开展,有些基础性的问题尚未解决,如天敌适应一种新的寄主资源所需要的时间和生态条件等。现有的研究多集中于茧蜂、蚜茧蜂、肿腿蜂、金小蜂等寄生蜂的某些种类,其它类群的寄生性天敌昆虫则涉及的较少,所研究的内容多为寄生率、寄主选择性、繁殖力等行为学和生态学上的观察记录,而对于生理生化、生存能力、遗传物质、资源利用率等方面的研究较少。因此,今后应加强这些基础问题的深入研究,扩大研究对象和范围,使研究结果更具有代表性,为生产上有效利用寄生性天敌提供必要的理论指导。

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