

拟寄生蜂搜索产卵过程中对寄主的竞争

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摘要:综述拟寄生蜂搜索产卵过程中对寄主竞争的最新研究进展。这类竞争具有四种方式,即标记寄主、杀卵和杀幼、守护寄主和捕食寄主。(1) 标记寄主常涉及寄主标记信息素,这是由雌蜂在产卵前、产卵时或产卵后分泌的化学物质。寄主标记信息素常介导拟寄生蜂对已寄生和健康寄主的辨别、减少过寄生和多寄生、减轻种内和种间竞争压力。(2) 雌蜂遇到已寄生寄主时,很多种类杀死前一雌蜂遗留的卵和幼虫,再产下自己的卵。雌蜂使用三种方法杀卵和杀幼,即产卵器穿刺、取食和使用有毒物质。通过杀卵和杀幼,产卵雌蜂清除了前一雌蜂遗留的后代,主动改善了寄主品质,从而有利于自身后代的生存。(3) 守护寄主在肿腿蜂科、缘腹细蜂科、金小蜂科、缨小蜂科和茧蜂科中均有报道,守护者驱逐入侵者以保护后代及健康寄主。(4) 捕食寄主不仅减少了健康寄主数量,且直接导致已寄生寄主中拟寄生蜂卵和幼虫的死亡。雌蜂一般在体内成熟卵量较少时捕食寄主。讨论了研究拟寄生蜂搜索产卵过程中竞争寄主的理论意义和实际应用价值。

关键词:拟寄生蜂;寄主标记;杀卵和杀幼;寄主守护;寄主捕食

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Competition among parasitoids for host during foraging and oviposition

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Abstract: During foraging and oviposition, hymenopteran parasitoid females often compete for hosts with individuals of the same or different species. The competition involves four types of behaviors: host-marking, ovicide or infanticide, brood-guarding and host-feeding. Advances in research of these behaviors are presented in detail in this review. (1) Host-marking has been documented in about 200 hymenopteran parasitoid species in nearly every super-family. Wasps mark exploited hosts physically or chemically before, during or after oviposition. However, most parasitoids utilize chemical markers, which are defined as host-marking pheromones (HMPs) or oviposition-detering pheromones. HMPs usually mediate the discrimination between parasitized and healthy hosts, reduce super- and multiparasitism, and minimize intra- and inter-specific competition. HMPs can often decrease the tendency for a wasp to lay eggs in a marked host and promote dispersal. When HMPs do not completely suppress oviposition, they can reduce clutch size. Moreover, a gregarious wasp may modify the sex ratio of deposited brood in response to the presence or absence of an HMP. (2) Ovicide or infanticide refers to a parasitoid destroying an existing clutch of eggs or larvae in a parasitized host before laying its own clutch. A wasp usually commits ovicide or infanticide either by piercing eggs or larvae with its ovipositor, eating them, or injecting a toxic substance to the first brood(s) before or during oviposition. Generally, an adult kills brood(s) on conspecifically parasitized hosts more frequently than on hosts parasitized by itself. Ovicide and infanticide are advantageous since they remove the competitor(s) to restore, at least partially, the quality of parasitized hosts. (3) Brood-guarding behaviors are observed in many species in the family Bethyridae, Scelionidae, Pteromalidae, Mymaridae and Braconidae. Guarding wasps attempt to repel intra- and inter-specific intruders to protect their broods or unexploited hosts. (4) Adults of some

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parasitoids feed on host insects to obtain energy to develop eggs, a behavior defined as host feeding. A host-feeding wasp consumes healthy hosts or even directly kills the parasitoid broods in previously parasitized hosts. Females tend to feed on hosts when they possess lower egg loads than higher egg loads. The theoretical importance and potential applications of host competition during foraging and oviposition among hymenopteran parasitoids are also discussed.

Key words: Hymenopteran parasitoid; host-marking; oviduct and infanticide; brood-guarding; host-feeding

拟寄生蜂是大多数自然和农田生态系统中植物-害虫-天敌动态关系的关键因素,是开发绿色、安全生物防治措施的首选对象。拟寄生蜂的种内和种间竞争及植物、气候条件、农事操作和栽培制度对这一竞争关系的影响,往往决定着拟寄生蜂控制害虫的有效性,因而成为目前昆虫学的热点研究领域之一^[1,2]。竞争是指两个或更多个体为了同一资源而展开的争夺^[3]。竞争分为冲突和利用两种形式。利用竞争(exploitation competition)是多个竞争者占据一个资源后对该资源的同时利用^[4],如群寄生(gregarious parasitism)、过寄生(super-parasitism)或多寄生(multi-parasitism)的拟寄生蜂幼虫对寄主食物的抢用。冲突竞争(interference competition)是间接或直接限制竞争对手接近资源的任何行动^[4]。拟寄生蜂搜索产卵过程中对寄主的竞争均为冲突竞争,常涉及标记寄主、杀卵和杀幼、守护寄主和捕食寄主四种行为。其中标记寄主属于间接冲突;杀卵和杀幼、守护寄主则为直接冲突;拟寄生蜂捕食已寄生寄主直接杀死了其中(上)的拟寄生蜂后代,是直接冲突;而捕食健康寄主减少了可用于产卵的寄主数量,是间接冲突。本文系统介绍拟寄生蜂搜索产卵过程中竞争寄主的研究进展。

1 寄主标记

寄主标记是雌蜂搜寻寄主时、产卵前、产卵时或产卵后遗留在寄主体内、体表或周围环境中的多种物理和化学信号。物理信号指雌蜂的搜寻和产卵活动在寄主表面或周围环境中留下的伤口、划痕、突起等^[5-8]。化学标记是一类昆虫产卵相关的信息化合物,称为寄主标记信息素(host marking pheromone)。已报道的例子中,绝大多数拟寄生蜂使用化学标记^[9,10]。据不完全统计,分布于姬蜂总科、小蜂总科、细蜂总科、肿腿蜂总科、腰蜂总科的200种以上的雌蜂均利用寄主标记辨认已寄生寄主^[7,9,10],避免过寄生和多寄生,减少种内和种间竞争。

1.1 寄主标记与种内竞争

1.1.1 阻止过度寄生 寄主标记最常见的作用是阻止过度寄生,驱避怀卵雌蜂,从而减少后代的食物竞争。单寄生蜂(solitary parasitoids)常被寄主标记信息素驱离,寻找未标记寄主^[9,10]。而多数群寄生蜂(gregarious parasitoids)可根据标记量判断寄主的利用程度,以决定是否产卵及产卵数量。如黑卵蜂 *Telenomus fariai* 产卵量大时,标记寄主的时间便长,这使后来的雌蜂可根据标记量判断寄主的质量^[11]。岭南黄蚜小蜂 *Aphytis lingnanensis*、印巴黄蚜小蜂 *A. melinus* 和黄蚜小蜂 *A. coheni* 在夹竹桃蚜中的产卵量与寄主体内已存卵量呈负相关^[12],表明标记可阻止后来者对寄主的过度利用。具有相似现象的还有腰蜂 *Pseudeucoila bochei*^[13] 和 *Leptopilina heterotoma*^[14] 及广赤眼蜂 *T. evanescens*^[15]。此外,寄主标记信息素还激发雌蜂逃离正在搜寻的区域,寻找新的产卵场所^[16-20]。有的拟寄生蜂还能够根据标记鉴别搜索与未搜索区域^[16,21],提高搜索效率,扩大竞争优势。

1.1.2 调节性比 拟寄生蜂寄主标记还能激发后来者调整卵的性比。一般地,随着寄主体内卵或幼虫的增加,雌蜂常多产雄性卵或少产雌性卵。这一现象在无臂茧蜂 *Asobara tabida*^[22]、丽蝇蛹集金小蜂 *Nasonia vitripennis*^[23]、广赤眼蜂 *T. evanescens*^[24]、缨小蜂 *Anaphes victus*^[25]、*A. nitens*^[26] 和黑卵蜂 *Telenomus fariai*^[27] 中发现。

1.1.3 鉴别亲缘关系 有些拟寄生蜂能根据标记信息素鉴别自身和同种其它雌蜂所产卵,避免自过寄生(self super-parasitism,同一雌蜂多次在同一寄主上产卵而引起的过寄生)^[28]。缨小蜂 *Anaphes iole* 遇到自寄生寄主时,往往重新标记寄主,自过寄生率只有20%;但遇到非自身寄生寄主时,过寄生率达到80%^[29]。缨小蜂 *A. n. sp.*^[30] 和 *A. victus*^[1]、黑卵蜂 *Telenomus busseolae* 和 *T. isis*^[31]、金小蜂 *Dinamus basalis*^[32]、跳小蜂 *Epidinocarsis*

lopezi^[33]、粉虱丽蚜小蜂 *Encarsia formosa*^[34]、*Eretmocerus eremicus* 和浆角蚜小蜂 *E. mundus*^[2]、卡氏盾痣细蜂 *Dendrocerus carpenteri*^[35]、姬蜂 *Venturia canescens*^[36]、蚜茧蜂 *Ephedrus californicus*^[37]、蚜茧蜂 *Aphidius pseudococci*^[38]、蚜外茧蜂 *Praon pequodorum*^[39] 等也具有相同的鉴别能力,避免自过寄生。辨认自身和同种其它雌蜂的卵具有适应性意义,因为与非自身卵共存时是不同基因型之间的竞争,若竞争不造成后产卵的死亡,则过寄生仍能获得一定的收益。而自过寄生则是兄弟姐妹之间的竞争,一般情况下只造成卵和时间的浪费,没有净收益^[33]。

拟寄生蜂还可根据寄主标记信息素区分亲缘关系的远近,避免与亲缘关系较近的个体竞争健康寄主。如缨小蜂 *A. victus*^[1] 和姬蜂 *Venturia canescens*^[36] 均能鉴别同胞、非同胞和不同地理品系的标记信息素。蝇蛹泛金小蜂 *Pachycropeus vindemmiae* 法国 Lyon 品系感受寄主内部的标记信息素;而 Rennes 品系只需用产卵器上的感受器检测寄主表面^[40]。这种差异可否区分亲缘关系,尚需研究。

拟寄生蜂通过寄主标记信息素的何种差异来区分亲缘关系的远近因种类而异,涉及 3 种机制。①双组分标记。如卡氏盾痣细蜂 *Dendrocerus carpenteri*^[35] 和沟卵蜂 *Trissolcus basalis*^[41] 的寄主标记信息素由高挥发性短效组分和低挥发性长效组分构成。当雌蜂在某处产卵时,这一区域可能同时存在自身和非自身寄生的寄主,非自身寄生的寄主由前一雌蜂遗留,寄生时间已较长,寄主上的高挥发性组分已散失;自身寄生的寄主因卵刚产下,高挥发性组分仍存在。雌蜂据此区分自身与非自身标记。②有的拟寄生蜂同时利用信息素标记寄主的外部 and 内部,随后到达的雌蜂可据此区分不同亲缘关系的个体。如缨小蜂 *Anaphes victus* 外部检测能区分同胞和非同胞标记,若同时检测外部和内部,能区分不同地理品系(Quebec、Taxes 和 Michigan 品系)的标记^[1]。③有的拟寄生蜂标记信息素混合物的组成比例在不同个体间存在可遗传的差异,这种差异可用来区分不同个体的标记。如姬蜂 *Venturia canescens* 的标记信息素碳氢化合物的种类和组成比例的差异与亲缘关系相关,雌蜂据此辨别亲缘关系的远近^[36]。

2.1 寄主标记与种间竞争

2.1.1 同属内不同种的竞争 寄主标记信息素可使拟寄生蜂进行种间鉴别。同一属的雌蜂相互感知对方的寄主标记信息素的实例较多。这类种间鉴别一般是不对称的,优势种常忽略劣势种的寄主标记信息素,而劣势种对优势种的寄主标记信息素反应灵敏,避免多寄生。如劣势种 *Eretmocerus eremicus* 检测标记信息素后完全拒绝被优势种浆角蚜小蜂 *E. mundus* 寄生的寄主,但优势种 *E. mundus* 却不拒绝被劣势种 *E. eremicus* 寄生的寄主^[2]。同样,缨小蜂 *Anaphes* n. sp. 和 *A. listronoti*^[30]、*A. victus* 和 *A. listronoti*^[1]、黑卵蜂 *Telenomus busseolae* 和 *T. isis*^[31]、无臂茧蜂 *Asobara tabida* 和 *A. rufescens*^[42]、无网长管蚜茧蜂 *Aphidius ervi* 和 *A. smithi*^[43,44]、卡氏盾痣细蜂 *Dendrocerus carpenteri* 及 *D. laticeps*^[45]、跳小蜂 *Epidinocarsis lopezi* 及 *E. diversicornis*^[46] 等事例中,劣势种均能感受到优势种的寄主标记信息素,避免多寄生。

2.1.2 不同属的竞争 同域发生、寄主彼此重叠的不同属拟寄生蜂也能感受对方的寄主标记信息素,竞争相同的食物资源。这类种间竞争也常常不对称。如多寄生对纹翅赤眼蜂 *Lathromeris ovicida* 的影响较小,而对黑卵蜂 *Telenomus isis* 的影响很大。当竞争共同寄主非洲大螟卵时, *L. ovicida* 忽略 *T. isis* 的标记导致多寄生,而 *T. isis* 对 *L. ovicida* 的标记反应灵敏,避免多寄生^[47]。金小蜂 *Dinamus basalis* 和旋小蜂 *Eupelmus vuilleti* 同域寄生豆象时,劣势种 *D. basalis* 可检测到优势种 *E. vuilleti* 的标记,而优势种 *E. vuilleti* 忽略劣势种 *D. basalis* 的标记^[48]。相似的现象还见于岛弯尾姬蜂 *Diadegma insulare* 和侧沟茧蜂 *Microplitis plutellae* 竞争小菜蛾幼虫^[49]、点缘跳小蜂 *Copidosoma truncatellum* 和粉蝶侧沟茧蜂 *Microplitis brassicae* 竞争粉纹夜蛾^[50]、蝇金小蜂 *Muscidifurax zaraptor* 和金小蜂 *Urolepsis rufipes* 竞争家蝇^[51]、蚜茧蜂 *Aphidius matricariae* 和蚜茧蜂 *Ephedrus cerasicola* 竞争桃蚜^[52]、无网长管蚜茧蜂 *Aphidius ervi* 和苜蓿斑蚜蚜小蜂 *Aphelinus asychis* 竞争蚜虫^[53] 等例子中。

2 杀卵和杀幼行为

雌蜂遇到已寄生寄主后,通过杀卵(幼)移除前一雌蜂留下的后代,主动改善寄主品质,再产下自己的卵。这避免了后代的种内和种间竞争,具有适应性意义。雌蜂的杀卵(幼)行为至今虽未深入研究,但现有报道已广泛涉及金小蜂科、蚜小蜂科、姬蜂科、茧蜂科和肿腿蜂科拟寄生蜂^[54]。

2.1 杀卵和杀幼方式

拟寄生蜂采用 3 种方式杀卵(幼)。其一是用产卵器刺破卵或幼虫。这种方式在外寄生(ecto-parasitoids, 产卵于寄主体表的拟寄生蜂)种类如螯蜂 *Echthrodolphax fairchildii*^[55]、瘤角姬蜂 *Pleolophus indistinctus*^[16]、蝇蛹泛金小蜂 *Pachycrepoideus vindemmiae*^[56] 和旋小蜂 *Eupelmus vuillei*^[57], 内寄生(endo-parasitoids, 产卵于寄主体内的拟寄生蜂)种类如单节螯蜂 *Haplogonatopus atratus*^[58,59] 和丽蚜小蜂 *Encarsia formosa*^[60,61] 中均有报道。其二是吃掉或用口器移除前一雌蜂遗留在寄主上的卵或幼虫。这常见于肿腿蜂科的外寄生蜂, 如棱角肿腿蜂 *Goniozus marasmii*^[62]、*G. platynotae*^[63,64]、*G. triangulifer*^[65] 和 *G. nephantidis*^[66]、肿腿蜂 *Laelius pedatus*^[67]、*Sclerodermus macrogaster*^[68] 和 *Cephalonomia hyalinipennis*^[69]。拟寄生蜂杀卵(幼)的第 3 种方式是在产卵过程中注入有毒物质杀死前一雌蜂遗留在寄主体内的后代^[70]。

2.2 杀卵和杀幼的进化条件

寄生卵和幼虫的易检测性是雌蜂是否采用杀卵(幼)策略的先决条件^[67]。外寄生蜂遗留的卵或幼虫极易被发现。少数内寄生蜂实例如单节螯蜂 *Haplogonatopus atratus* 卵粘附于产卵部位的体壁之下直至 2 龄末期, 极易被发现^[58]。内寄生蜂丽蚜小蜂 *Encarsia formosa* 的卵较大, 达寄主粉虱体长的 1/4 ~ 1/3, 且粉虱身体扁平, 寄生卵也易被发现^[61]。

采用进化上的稳定策略模型, 推断群寄生蜂采取杀卵(幼)策略的条件为: (1) 杀卵(幼)需时较短; (2) 健康的可用于产卵寄生的寄主稀缺; (3) 先产卵处于竞争优势^[71]。实验数据证明了这一推断。如麦蛾茧蜂 *Bracon hebetor* 杀卵需时只占产卵时间的 1/6 左右^[71], 先产卵竞争优势明显^[72], 在健康寄主稀少时杀卵率高^[71,72]。蝇蛹泛金小蜂 *Pachycrepoideus vindemmiae* 杀卵后再产卵与直接产卵需时相当, 杀卵频率负相关于健康寄主数量^[56]。螯蜂 *Echthrodolphax fairchildii* 杀幼仅需 10 s, 杀幼率与先产卵的竞争优势正相关^[55]。肿腿蜂 *Laelius pedatus* 先产卵的竞争优势也非常明显, 杀卵后再产卵所用时间仅略长于直接产卵^[67]。单节螯蜂 *Haplogonatopus atratus*^[58] 和丽蚜小蜂 *Encarsia formosa*^[61] 杀卵需时均较短。

2.3 影响杀卵和杀幼的因素

杀卵和杀幼行为受多种其它因素的影响。蝇蛹泛金小蜂 *Pachycrepoideus vindemmiae* 杀卵行为受寄主种类的影响。寄生黑腹果蝇蛹时, 杀卵率较高, 且与蛹寄生率正相关。而寄生实蝇 *Delia radicum* 时, 杀卵率较低且不随蛹寄生率变化^[56]。此外, 麦蛾茧蜂 *Bracon hebetor*^[73]、单节螯蜂 *Haplogonatopus atratus*^[58] 和螯蜂 *Echthrodolphax fairchildii*^[55] 均能辨认出自身所产卵, 避免杀死自己的后代。

2.4 杀卵(幼)与种间竞争

杀卵和杀幼还与拟寄生蜂的种间竞争有关。如旋小蜂 *Eupelmus vuillei* 倾向产卵于被金小蜂 *Dinarmus basalis* 寄生的豆象幼虫上, 产卵前杀死竞争对手 *D. basalis* 的卵^[57]。肿腿蜂 *Cephalonomia hyalinipennis* 和 *C. stephanoderis* 遇到携带有对方卵的咖啡果小蠹虫后, 常取食对方的卵后再产下自己的卵^[69,74]。

3 寄主守护行为

3.1 守护行为的类型

有些拟寄生蜂遇到健康可产卵寄生的寄主后, 常滞留在寄主周围, 驱逐随后到达的产卵雌蜂, 等待卵的成熟而最终产卵。如棱角肿腿蜂 *Goniozus nephantidis* 遇到织蛾 *Opisina arenosella* 幼虫后, 钻入 *O. arenosella* 巢穴并麻醉寄主, 作为拥有者守护寄主 1 ~ 3d 后再产卵。在此期间, 拥有者常追逐并袭击入侵者, 直至失败者逃离巢穴为止。两个因素决定最后的胜利者。其一是拥有者身分, 在角斗时, 拥有者的获胜率是入侵者的 1.32 倍。其二是体重, 若拥有者体重较大, 入侵者不能替代拥有者; 而当入侵者体重大时, 替代率与体重差异正相关^[66,75]。这两个取胜因素均与寄主守护期有关, 在守护期间, 拥有者体内的卵粒迅速成熟。这不仅增加了拥有者的产卵欲望, 同时增大了体重, 这是拥有者获胜几率高的原因之一^[76]。

寄主守护行为若发生在产卵后, 则是看护后代。棱角肿腿蜂 *Goniozus nephantidis* 产卵后, 停息在寄主巢穴内直至其后代化蛹^[66,76]。棱角肿腿蜂 *G. legneri* 具有相似的行为^[66]。肿腿蜂 *P. nasuta* 看护时用咖啡果小蠹

虫成虫的尸体堵塞咖啡果上的蛀孔,阻止其它拟寄生蜂的进入^[77]。沟卵蜂 *Trissolcus basalis* 寄生一个卵块不到 1 h,但后代看护持续 2~5 h^[78~81]。肿腿蜂 *C. stephanoderis*^[69]、金小蜂 *Erixestus uinnemana*^[82] 也具有类似的后代看护行为。

有的拟寄生蜂寄生卵块或生活在一起的幼虫,拟寄生蜂的一次产卵只能寄生这些寄主的一部分,此时守护寄主既是对健康寄主的占领,又是对后代的看护。如 3 种柄翅小蜂 *Gonatocerus ashmeadi*、*G. truguttatus* 和 *G. fasciatus* 在大叶蝉 *Homalodisca coagulata* 卵块上一次产卵后,逗留在寄主附近休息、清洁触角及身体,随后回到卵块上继续产卵,在此过程中守护寄主、驱逐同种或不同种入侵者^[83]。肿腿蜂 *Cephalonomia stephanoderis*、*C. hyalinipennis* 和 *Prorops nasuta* 分批产卵寄生生活在一起的咖啡果小蠹虫时,均守护寄主,当同种或异种雌蜂入侵时,拥有者和入侵者之间发生角斗,采用追逐、叮咬和螫刺攻击对方^[84]。同种角斗并不引起死亡。而异种角斗时,获胜者常将螫针刺入对方体内,麻醉并杀死对方^[74,84]。相似的寄主守护和攻击行为还在棱角肿腿蜂 *Goniozus nephantidis* 和麦蛾茧蜂 *Bracon hebetor* 竞争寄主时发现^[66]。

3.2 采用守护行为的条件

拟寄生蜂是否采用寄主守护及守护的时间长短与守护的后代数量密切相关。群寄生蜂(gregarious parasitoids)或准群寄生蜂(quasi-gregarious parasitoids, 寄主群聚的单寄生蜂)比单寄生蜂更为经济,故更倾向于采用寄主守护^[80]。肿腿蜂 *Cephalonomia stephanoderis* 对只有 1~3 个后代的寄主看护时间短,而对具有多个后代的寄主看护时间长^[69]。

寄主守护和争夺行为有的较为温和,如驱逐和炫耀,失败者并无明显的伤残;有的较为激烈,常造成明显伤残甚至死亡。博弈论模型分析表明,若拟寄生蜂随后可能遇到的寄主好于或多于正在争夺的寄主,选择温和和争夺行为。相反,若寄主极为稀缺,随后可能遇到的寄主等于或差于正在争夺的寄主,则选择激烈争夺行为^[85~87]。

4 捕食行为

4.1 捕食行为的类型

有些拟寄生蜂有时用产卵器刺穿可用于产卵寄生的寄主,使血淋巴外渗,然后取食血淋巴^[88,89]而导致寄主的死亡。如肿腿蜂 *Cephalonomia stephanoderis*、*C. hyalinipennis* 和 *Prorops nasuta* 羽化后需捕食寄主咖啡果小蠹虫,卵粒才分批成熟。这 3 种肿腿蜂均嗜食卵和低龄幼虫。*C. stephanoderis* 的捕食率在笼罩时达到 65%,田间观察达 49%^[90~92]。田猎姬蜂 *Agrothereutes lanceolatus* 取食寄主常引起寄主的麻痹和死亡^[93]。此外,取食寄主的还有丽蚜小蜂 *Encarsia formosa*^[61]。

拟寄生蜂也捕食被寄生的寄主,故捕食也杀死了同种或不同种拟寄生蜂的后代。如田猎姬蜂 *Agrothereutes lanceolatus* 捕食被寄生的几种螟蛾和卷蛾的老熟幼虫、预蛹和蛹时,杀死了绝大部分的同种寄生卵^[93]。肿腿蜂 *Cephalonomia hyalinipennis*、*C. stephanoderis* 或 *Prorops nasuta* 捕食咖啡果小蠹虫时,杀死寄主体内的同种或异种拟寄生蜂卵^[69,77]。

4.2 影响捕食行为的因素

拟寄生蜂是否捕食寄主受载卵量、遇到健康寄主频率等因素的影响。如田猎姬蜂 *Agrothereutes lanceolatus* 当体内成熟卵量极少时,需大量营养满足卵的发育,此时大量捕食寄主。而当体内成熟卵较多时,则不捕食或很少捕食寄主。此外,田猎姬蜂 *A. lanceolatus* 捕食寄主的频率还与遇到健康寄主的次数有关,单位时间内遇到健康寄主的次数越多,捕食次数越多^[93]。

5 展望

拟寄生蜂搜索产卵过程中竞争寄主的行为和方式是昆虫中乃至动物中最为复杂和完善的,这为研究动物行为反应、调控途径及进化路线提供了理想的研究材料。同时,拟寄生蜂搜索产卵过程中竞争寄主的研究也有广泛的实际应用价值。首先,拟寄生蜂搜索产卵过程中竞争寄主的能力是拟寄生蜂能否有效控制害虫的关键评估指标,其研究结果为合理利用拟寄生蜂进行生物防治提供了重要依据^[2,69,74]。其次,搜索产卵过程中竞

争寄主是拟寄生蜂种间竞争的重要手段,是评估不同种拟寄生蜂协同控制同一种害虫的重要指标。比较欲引种和当地种对健康寄主的竞争,可避免引入能抑制甚至灭绝当地种的拟寄生蜂^[31,69,74]。

相比上述理论意义和应用价值,拟寄生蜂搜索产卵过程中竞争寄主的研究还远远不够。目前外国的研究大都限于现象的描述和解释,对深层次的问题如拟寄生蜂搜索产卵过程中竞争寄主的选择压力和进化路线、行为的生理生化机制及基因调控等,鲜有报道。而在我国,这一领域的研究刚刚起步,如寄主标记现象在多种黑卵蜂^[94~96]、长棒四节蚜小蜂 *Pteroptrix longiclava* 和黄胸扑虱蚜小蜂 *Encarasis gigas* 中发现^[97]。刘展羲等^[98]最近报道芦苇格姬小蜂 *Phygadeuon phragmitis* 产卵前捕食寄主。可见,拟寄生蜂搜索产卵过程中竞争寄主的研究方兴未艾,尚需昆虫学、生态学、生理学、生化学、分子生物学和遗传学等多门学科专家的努力和协同攻关。

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