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# 生 态 学 报

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**封面图说**:站立的仓鼠——仓鼠为小型啮齿类动物,栖息于荒漠、荒漠草原等地带的洞穴之中。白天他们往往会躲在洞穴中睡觉和休息,以避开天敌的攻击,偶尔也会出来走动,站立起来警惕地四处张望。喜欢把食物藏在腮的两边,然后再走到安全的地方吐出来,由此得仓鼠之名。它们的门齿会不停的生长,所以它们的上下门齿必须不断啃食硬东西来磨牙,一方面避免门齿长得太长,妨碍咀嚼,一方面保持门牙的锐利。仓鼠以杂草种子、昆虫等为食。

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周慧, 张扬, 吴伟坚. 稻纵卷叶螟绒茧蜂对寄主的搜索行为. 生态学报, 2012, 32(7): 2223-2229.

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# 稻纵卷叶螟绒茧蜂对寄主的搜索行为

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**摘要**: 稻纵卷叶螟绒茧蜂是稻纵卷叶螟幼虫的重要天敌。以 Y 形嗅觉仪测定了稻纵卷叶螟 2—3 龄幼虫虫粪、4—5 龄幼虫虫粪、健康水稻、稻纵卷叶螟幼虫为害后水稻在纵卷叶螟绒茧蜂对寄主的搜索过程中的作用。结果表明已交配的雌蜂显著趋向稻纵卷叶螟 2—3 龄幼虫虫粪和 4—5 龄幼虫虫粪,不趋向健康水稻、稻纵卷叶螟幼虫为害后的水稻。雄蜂、处女雌蜂不显著趋向健康水稻、稻纵卷叶螟幼虫为害后水稻、稻纵卷叶螟 2—3 龄幼虫虫粪、稻纵卷叶螟 4—5 龄幼虫虫粪。利用固相微萃取(SPME)及气相色谱/质谱(GC/MS)联用分析稻纵卷叶螟 2—3 龄幼虫虫粪的化学成分,并通过 Y-形嗅觉仪测试已交配雌蜂对稻纵卷叶螟 2—3 龄幼虫虫粪化学成分标准品的嗅觉反应,结果表明已交配的雌蜂显著趋向 1-十一烯和异缬草醛,稻纵卷叶螟幼虫虫粪中的 1-十一烯和异缬草醛可能是稻纵卷叶螟绒茧蜂搜索寄主的利他素。

**关键词**: 稻纵卷叶螟绒茧蜂; 寄主搜索行为; 虫粪; 利他素

## Host searching behaviour of *Apanteles cypris* Nixon (Hymenoptera: Braconidae)

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**Abstract**: *Apanteles cypris* Nixon is one of the most important natural enemies of the larvae of rice leaf folder, *Cnaphalocrocis medinalis* Guenée. Through parasitizing their larvae, *A. cypris* wasps play a major role in biological control of *C. medinalis*; parasitized host larvae consume less rice leaf than non-parasitized counterparts, thus causing less damage. Previous studies suggest that some parasitoids using chemical cues to locate their hosts. In a tritrophic interaction system consisting of plants, herbivores, and their parasitoids, chemicals released from plants after herbivory are known to help many female parasitoids find their hosts efficiently. Chemical information associated with herbivory can act as an indirect defense for the plant by attracting natural enemies of the host herbivores. There are several potential sources of infochemicals used by parasitoids: the host plant, direct or indirect cues from the host. This study aims to determine if the host searching behavior of *A. cypris* is affected by volatiles from *C. medinalis*-infested and uninfested rice plants and frass produced by larvae of *C. medinalis*. We found that mated female *A. cypris* were attracted by the frass of 2nd/3rd or 4th/5th instar *C. medinalis* larvae but not by *C. medinalis*-infested and uninfested rice plants. In contrast, male and virgin female *A. cypris* did not respond significantly to any of the stimuli. These results indicate that the mating status of *A. cypris* females clearly influences their host-searching behavior in response to herbivory-associated chemical information, and we suggest that female parasitoids forage for hosts depending on their own physiological condition in a tritrophic system. To elucidate which chemicals are used by *A. cypris* to locate their hosts, we analyzed the chemical composition of frass produced by 2nd/3rd instar *C. medinalis* larvae using solid-phase micro-extraction (SPME) combined with gas chromatography/mass

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spectrometry (GC/MS). We collected 23 volatiles from the frass, including terpenoids, alcohols, ketones, amines, aldehyde. Chemical standards of the determined frass components are then tested for the chemotactic effect on mated female *A. cypris* using Y-tube olfactometer. We found that mated female *A. cypris* were significantly attracted by 1-undecene and 3-methylbutanal, and suggest that these compounds in the frass of *C. medinalis* larvae are the kairomones that attract endoparasitoid *A. cypris*. Our results may prove to be helpful for the agricultural industry through use of these kairomones as control agents for *C. medinalis*, and are the basis of further study into the tritrophic system of rice -*C. medinalis*-*A. cypris* and development of new control methods.

**Key Words**: *Apanteles cypris*; host searching behavior; frass; kairomone

寄生蜂在搜索寄主的过程中,信息化合物起着重要作用,它们可利用寄主植物、植食性昆虫的信息化合物以及植食性昆虫取食寄主后诱导产生的信息化合物来寻找寄主[1-8]。特别是对隐藏为害的寄主昆虫的寻找,挥发性物质起着更为重要的作用[9],所以探明不同来源挥发物的组成是研究三级营养关系化学通讯的先决条件。利他素、协同素和标记信息素是目前研究较多的三类信息化合物[10-11]。其中来源于寄主本身的被称为利他素的信息化合物在寄生蜂寻找寄主的过程中起着关键作用,它存在于寄主的不同部位或不同时期,如寄主卵、翅的鳞片、性信息素、成虫及其排泄物等[1, 12]。对于一个进行寄主搜寻的寄生蜂来说,如何利用挥发物提供的信息成为成功寄生的关键所在。

近年来,有关寄生蜂对信息化合物的行为反应及学习经历的研究日益受到重视。稻纵卷叶螟绒茧蜂(*Apanteles cypris* Nixon)属膜翅目茧蜂科,是热带和亚热带地区水稻主要害虫[13]——稻纵卷叶螟(*Cnaphalocrocis medinalis* Guenée)幼虫的重要寄生性天敌,主要寄生稻纵卷叶螟2龄幼虫,具有专一性、单寄生、寄生率较高等特点[14]。稻纵卷叶螟幼虫被稻纵卷叶螟绒茧蜂寄生后,通常活性减弱,取食量大大减少,大多在暴食期前死亡,因此稻纵卷叶螟绒茧蜂具有很高的保护利用价值[15-16]。

本研究旨在探讨水稻—稻纵卷叶螟—稻纵卷叶螟绒茧蜂三级营养关系中寄生蜂搜索寄主的信息化合物,进一步分析寄生蜂对寄主的搜索机理,为保护、扩繁释放和招引稻纵卷叶螟绒茧蜂以防治害虫提供科学依据。

## 1 材料和方法

### 1.1 供试材料

#### 1.1.1 供试昆虫

寄主昆虫:稻纵卷叶螟采自华南农业大学农场,在人工气候养虫室(25±1)℃;*RH*: 60%—80%;16L∶8D;光照强度 >1000 lx 进行饲养。

寄生蜂:华南农业大学农场收集稻纵卷叶螟绒茧蜂蜂茧,羽化后用10%的蜂蜜水补充营养,以羽化后2—3 d的雌雄蜂配对,交配1 d后的雌蜂供试。处女雌蜂、雄蜂采用同天羽化未交配雌蜂及雄蜂,所有供试昆虫均在(28 ± 1) ℃;*RH*: 60%—80%;16L∶8D 光周期条件下饲养。

#### 1.1.2 供试水稻

水稻品种为IR36,种子由广东省农科院植物保护研究所提供。分蘖期苗高30 cm时用于实验。

#### 1.1.3 试验仪器

美国Supelco公司生产100 μm PDMS的固相微萃取;日本岛津公司生产GC/MS-QP2010;根据稻纵卷叶螟绒茧蜂体型、大小等特点改进设计的Y型嗅觉仪[17-18]:嗅觉仪的两臂及直管均长10.00 cm,内径1.5 cm,两臂夹角75°,两臂距直管3 cm处为选择决定线。控制气流量在250 mL/min。

### 1.14 供试试剂

液体丙酮(衡阳市凯信化工试剂有限公司生产)、所用标准品均为德国Sigma-Aldrich公司生产,包括邻苯二甲酸二乙酯(99.5%)、二甲己胺(99%)、2-甲基-3-己醇(98%)、二苯甲酮(99%)、丙烯醛-4-羟基丁酯(90%)、1-甲基癸胺(97%)、2-甲基-1-戊醇(99%)、苯乙酮(≥99%)、麝香T(95%)、十一烯(97%)、异缬草

醛(97%)。

**1.2**　研究方法

**1.2.1**　稻纵卷叶螟绒茧蜂对寄主的搜索行为

单头稻纵卷叶螟绒茧蜂引入嗅觉仪,当蜂爬至超过某臂选择决定线并持续 30 s 以上,就记该蜂对该臂的气味源作出选择。如蜂引入 5 min 后仍不作出选择,则结束对该蜂的行为观察,并记为不反应,测试 30 头作出反应的绒茧蜂(测试条件:(27±2) ℃、*RH* 70%—80%、光强 500 lx,时间:21:00—2:00)。根据 McCall 和 Turlings 的方法清洗装置[2]。

味源设置:

健康水稻植株　取分蘖期 30 cm 高左右的健康植株水稻苗 10 株供试。

被害水稻植株　取健康分蘖期水稻苗,每盆接 2—3 龄稻纵卷叶螟幼虫 10 头,取食 48 h 后除虫除粪供试。

稻纵卷叶螟 2—3 龄幼虫虫粪　取健康分蘖期水稻苗,每盆接 2—3 龄稻纵卷叶螟幼虫 10 头,取食 48 h 后收集新鲜的虫粪 5 g。

稻纵卷叶螟 4—5 龄幼虫虫粪　取健康分蘖期水稻苗,每盆接 4—5 龄稻纵卷叶螟幼虫 10 头,取食 48 h 后收集新鲜的虫粪 5 g。

**1.2.2**　SPME-GC/MS 分析稻纵卷叶螟 2—3 龄幼虫虫粪挥发性成分

称取 10 g 稻纵卷叶螟 2—3 龄幼虫虫粪,放入 5 mL 的样品瓶中,用专用封口装置封口,备用。将 SPME 的萃取纤维头在气相色谱的进样口活化 30 min,活化温度为 250℃,活化后顶空萃取 30 min。插入 GC/MS 进样口,250 ℃热脱附样品进色谱柱。气相色谱条件 GC 条件:HP-5 弹性石英毛细管色谱柱(30 m×0.25 mm×0.25 μm)。升温程序:初始温度 40 ℃保持 2 min,以 5—250 ℃/min,保持 1 min,以 40—310 ℃/min,10 min。载气:氦气;载气流速 0.76 mL/min;进样口温度 250 ℃。质谱条件离子源为 EI,电离电压 70ev,离子源温度 250 ℃,溶剂延迟时间 2.5 min,质谱范围 35—500;扫描速度 1666。

样品瓶内放入虫粪前,在上述条件下进行检测,以去除杂质干扰。

**1.2.3**　稻纵卷叶螟绒茧蜂对虫粪挥发物化学成分标准品的反应

把购得虫粪挥发物主要化合物的 11 种标准品,全部稀释 1000 倍用 Y 型嗅觉仪测定标准品与空白对照的行为反应。选择标准以及测试方法同 1.2。

**1.3**　数据分析

嗅觉行为反应所有数据均采用 SPSS10.0 软件分析,以 $\chi^2$ 适合性检验分析寄生蜂趋向 Y 形嗅觉仪两臂的个体数是否符合比率 1:1。

## 2　结果与分析

**2.1**　稻纵卷叶螟绒茧蜂对寄主的搜索行为

与空白对照比,稻纵卷叶螟绒茧蜂雄蜂、已交配雌蜂、处女雌蜂对健康水稻植株、被害水稻株没有表现出明显的趋向性,表明稻纵卷叶螟绒茧蜂寻找寄主的活性物质不存在于健康水稻、稻纵卷叶螟幼虫为害水稻的挥发物中(图 1)。稻纵卷叶螟绒茧蜂已交配雌蜂显著趋向稻纵卷叶螟 2—3 龄幼虫虫粪、稻纵卷叶螟 4—5 龄幼虫虫粪,而稻纵卷叶螟绒茧蜂雄蜂以及处女雌蜂对寄主幼虫虫粪则没有趋性(图 2),表明稻纵卷叶螟 2—3 龄幼虫虫粪、稻纵卷叶螟 4—5 龄幼虫虫粪的挥发物中存在吸引纵卷叶绒茧蜂已交配雌蜂的活性物质。雄蜂不

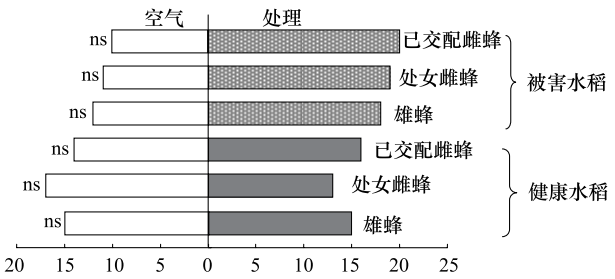


**图 1**　稻纵卷叶螟绒茧蜂对健康和受害水稻的嗅觉反应(ns:差异不显著)

**Fig. 1**　**Responses of male and female *Apanteles cypris* to leaf folder damaged and uninfested rice in 2-choice bioassays**(ns: not significant)

依赖虫粪中的信息化学物质寻找雌蜂,交配与否影响雌蜂对寄主的搜索行为。

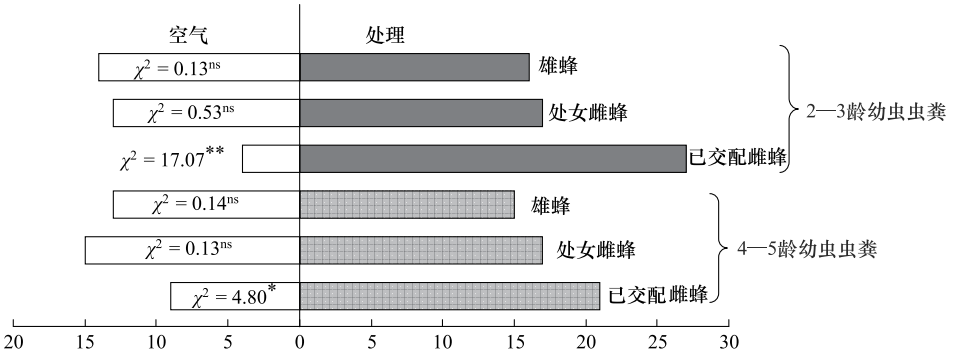


**图 2 稻纵卷叶螟绒茧蜂对幼虫虫粪的嗅觉反应**

**Fig. 2 Responses of *Apanteles cypris* to larval frass over control in a Y-tube olfactormeter. Significance levels of $\chi^2$ indicated by ns**

ns:差异不显著; * :$P<0.05$, 差异显著; * * :$P<0.01$,差异显著; ($P>0.05$), * ($P<0.05$), * * ($P<0.01$)

## 2.2 稻纵卷叶螟 2—3 龄幼虫虫粪挥发性成分

按照 1.2.3 的条件,得到 100μm PDMS-GC/MS 萃取头测定虫粪挥发物质成分(表 1)。

**表 1 100 μm PDMS 萃取头测定新鲜虫粪挥发物成分**

**Table 1 The main volatile components of fresh larvae fecula by 100μm PDMS-GC/MS**

| 编号 No. | 挥发性化学物质 Volatile chenmical compounds | 相似度 *SI* | 相对含量 Rel. Per. Com | 保留时间 *RT*/min |
|---|---|---|---|---|
| 1 | 2-甲基-1-戊醇、2-Methyl-1-pentanol | 89/88 | 0.29 | 6.210 |
| 2 | 二甲己胺 Octodrine | 90 | 0.09 | 8.095 |
| 3 | 1-甲基葵胺 1-Methyldecylamine | 90 | 0.12 | 9.016 |
| 4 | 2,2,6-三甲基环己酮 2,2,6-trimethyl-Cyclohexanone | 89 | 0.17 | 10.396 |
| 5 | 苯乙酮 1-phenyl-Ethanone | 85 | 0.09 | 11.309 |
| 6 | E-7-十四烯醇 E-7-Tetradecenol | 78 | 0.36 | 11.787 |
| 7 | 1-十一烯 1—Undecene | 96 | 18.42 | 12.008 |
| 8 | 1-(5-双环[2.2.1]庚烯)已胺 1-(5-Bicyclo[2.2.1]heptyl)ethylamine | 82 | 0.19 | 12.412 |
| 9 | 肾上腺酮 Adrenalone | 76 | 0.52 | 15.897 |
| 10 | 异缬草醛 3-Methylbutanal | 86 | 0.63 | 17.824 |
| 11 | 2-氨基十九烷 2-Amininonadecane | 77 | 0.23 | 18.765 |
| 12 | 黄藤内酯 Columbin | 74 | 0.84 | 20.732 |
| 13 | 1-(3,5-Dimethyl-1-adamantanoyl)semicarbazide | 70 | 0.33 | 21.716 |
| 14 | β-紫罗兰酮 beta. -Ionone | 87 | 0.62 | 22.968 |
| 15 | Z-alpha-trans-香柠檬醇 Z-. alpha. -trans-Bergamotol | 79 | 23.61 | 23.699 |
| 16 | 邻苯二甲酸二乙酯 Diethyl Phthalate | 87 | 2.76 | 25.217 |
| 17 | 十三碳二酸乙二醇酯 Ethylene brassylate | 74 | 12.57 | 26.206 |
| 18 | 2,6-二(1,1-二甲基)-4-(1-丙酰氨基)苯酚 2,6-Bis (1,1-dimethylethyl)-4-(1-oxopropyl)phenol | 84 | 3.74 | 26.294 |
| 19 | (1,7,7-三甲基双环[2.2.1]庚-2-基)二叔丁基氯化膦 (1,7,7-trimethylbicyclo[2.2.1]hept-2-yl)- Phosphonous dichloride | 86 | 3.51 | 27.039 |
| 20 | 顺式肉果草醇 cis -Lanceol | 87 | 10.71 | 29.220 |
| 21 | 4-十八吗啉 4-octadecyl-Morpholine | 94 | 12.12 | 31.650 |
| 22 | 10-羟基-11-对氧氮己环-4-十一烷酸异丙酯 10-hydroxy-11-morpholin-4-yl-Undecanoic acid isopropyl ester | 90 | 5.55 | 35.660 |
| 23 | N-正丁基-4,9-癸二烯-2-胺 N-butyl-4,9-Decadien-2-amine | 88 | 2.53 | 39.315 |

### 2.3　稻纵卷叶螟绒茧蜂的搜索利他素

稻纵卷叶螟绒茧蜂显著趋向 1-十一烯和异缬草醛（表 2),稻纵卷叶螟幼虫虫粪中的 1-十一烯和异缬草醛是稻纵卷叶螟绒茧蜂搜索寄主的利他素。

**表 2　稻纵卷叶螟绒茧蜂已交配雌蜂对虫粪挥发物化学成分标准品的趋性反应**

**Table 2　Preference of mated famle *A. cypris* to chemical standards over control in a Y-tube olfactormeter. Significance levels of $\chi^2$ indicated by ns**

| 标准品 Chemical standards | *n* | 选择虫数 Numbers/头 | | $\chi^2(P)$ |
|---|---|---|---|---|
| | | 处理 Tretment | 对照 CK | |
| 邻苯二甲酸二乙酯 Diethyl Phthalate | 30 | 18 | 12 | 1.200(0.273) |
| 二甲己胺 Octodrine | 30 | 17 | 13 | 0.533(0.465) |
| 十一烯 1-Undecene | 30 | 23 | 7 | 8.533(0.03) * |
| 2-甲基-3-己醇 2-Methy-3-hexanol | 30 | 17 | 13 | 0.533(0.465) |
| 异缬草醛 3-Methylbutanal | 30 | 24 | 6 | 10.800(0.01) ** |
| 二苯甲酮 Benzophenone | 30 | 14 | 16 | 0.133(0.715) |
| 丙烯醛-4-羟基丁酯 4-Hydroxybutyl acrylate | 30 | 19 | 11 | 2.133 (0.144) |
| 1-甲基癸胺 1-Methyldecylamine | 30 | 16 | 14 | 0.133(0.715) |
| 2-甲基-1-戊醇 2-Methyl-1-pentanol | 30 | 18 | 12 | 1.200(0.273) |
| 苯乙酮 1-phenyl-Ethanone | 30 | 15 | 15 | 0.000 (---) |
| 麝香 Tethylene brassylate | 30 | 16 | 14 | 0.133(0.715) |

($P$>0.05) or * ($P$ <0.05), * * ($P$ <0.01)

## 3　结论与讨论

寄生蜂在多异的环境中准确定位寄主是一系列复杂的繁殖策略综合作用的结果[9, 15, 19-21]。源于寄主或寄主植物的行为信息化合物对寄生蜂搜索寄主起到重要的作用[22-25]。寄生蜂倾向于在近距离搜索寄主时利用寄主本身的气味。相反,寄生蜂在远距离搜索时倾向于利用来源于寄主植物、寄主附属物(寄主唾液、寄主粪便、鳞片等)的信息化合物寻找寄主昆虫[26-30]。本研究表明,稻纵卷叶螟绒茧蜂显著趋向稻纵卷叶螟幼虫虫粪,不显著趋向水稻和被稻纵卷叶螟幼虫为害后的水稻,所以在水稻—稻纵卷叶螟—稻纵卷叶螟绒茧蜂所形成的三级营养关系中,以稻纵卷叶螟幼虫虫粪挥发物为主导的化学因子应起主要作用。已交配的雌蜂显著趋向稻纵卷叶螟 2—3 龄幼虫虫粪及稻纵卷叶螟 4—5 龄幼虫虫粪,这从一个侧面解析了稻纵卷叶螟绒茧蜂对稻纵卷叶螟 2—3 龄幼虫的寄生率高于稻纵卷叶螟 4—5 龄幼虫[14, 31]的原因,当然这种寄生率高低差异也可能与 4—5 龄幼虫有较强的抗寄生力和高龄幼虫临近化蛹有关。寄生蜂交配与否影响对信息化合物的感知,虫粪的挥发物仅对已交配稻纵卷叶螟绒茧蜂具引诱活性,与 Soichi[32]结果一致,原因有待于进一步研究。

进一步分析虫粪挥发物中引致稻纵卷叶螟绒茧蜂产生趋向反应的化学成分,结果表明稻纵卷叶螟绒茧蜂显著趋向 2 种化合物(1-十一烯 1-undecene,异缬草醛 3-methylbutanal)。胡京生等[33]认为稻纵卷叶螟绒茧蜂搜索利他素是由虫粪中 8 种氨基酸和海藻糖所组成,可能氨基酸类物质和挥发性物质都对纵卷叶螟绒茧蜂定位寄主起到重要作用,只是作用的方式或阶段不同,它们之间的关系还有待于进一步研究。

目前寄生蜂对寄主的搜索机理还没有一个普遍适用的理论,寄生蜂根据自身特点演化出选择寄主的策略和交配策略[26]。探讨稻纵卷叶螟绒茧蜂搜索寄主的机制,为更好的了解寄生蜂寄主定位机理提供新论据。在害虫天敌大量饲养和人工释放过程中,利他素可增进天敌寻找寄主的效率[34]。本文研究结果为 1-十一烯和异缬草醛作为保护和定向招引稻纵卷叶螟绒茧蜂防治稻纵卷叶螟的利他素提供重要的基础。以期从理论上进一步丰富寄生蜂搜索寄主机制。

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