

离腹寡毛实蝇两性通讯及行为

张秀歌, 张小娇, 肖 春*, 董文霞*

(云南农业大学植物保护学院, 云南生物资源保护与利用国家重点实验室, 昆明 650201)

摘要: 离腹寡毛实蝇属 *Bactrocera* spp. 实蝇对全世界的水果和蔬菜产生巨大的威胁, 造成严重的经济损失。传统的杀虫剂化学防治、不育技术 (sterile insect technique, SIT)、雄虫灭绝技术 (male annihilation technique, MAT) 一直是防控大多数实蝇的主要措施, 但具有一定的局限性。因此, 急需新的环保型防控方法来防治实蝇。为建立基于昆虫行为的防治策略, 本文对离腹寡毛实蝇 *Bactrocera* spp. 两性的生殖通讯及相关的行为进行了概述。总结了实蝇的交配系统以及雄虫在求偶之前在求偶炫耀场所的一系列行为, 阐述了雌虫交配后产卵标记行为和竞争单个产卵位置的行为以及未来的研究方向, 将为实蝇害虫综合治理提供新的思路及参考。

关键词: 离腹寡毛实蝇属; 交配系统; 求偶交配行为; 攻击性行为; 交配后雌虫行为

中图分类号: Q968 文献标识码: A 文章编号: 0454-6296(2017)11-1349-12

Sexual communication and behaviours in *Bactrocera* fruit flies (Diptera: Tephritidae)

ZHANG Xiu-Ge, ZHANG Xiao-Jiao, XIAO Chun*, DONG Wen-Xia* (College of Plant Protection, Yunnan Agricultural University, State Key Laboratory for Conservation and Utilization of Biological Resources in Yunnan, Kunming 650201, China)

Abstract: *Bactrocera* fruit flies are an enormous threat to fruit and vegetable production throughout the world, causing great economic loss. Although chemical control based on conventional insecticides and biotechnical tools including sterile insect technique (SIT) and male annihilation technique (MAT) have been the main weapons used in most control programs, they still have many restrictions, and ecofriendly control tools against *Bactrocera* spp. are urgently needed. Thus, current knowledge about sexual communication and related behaviours in *Bactrocera* spp. was reviewed in this article to help build behaviour-based control strategies. Two different polygynous mating systems in Tephritidae and behavioural sequences of males before courtship in lekking sites were summarized, and some mated female behaviours in oviposition sites, including oviposition marking behaviour and fighting behaviour for single oviposition sites, were elaborated. Future perspectives were also outlined. The knowledge about sexual communication is expected to provide new insights and references for integrated pest management programs for tephritid pests.

Key words: *Bactrocera*; mating systems; leks; aggressive behaviour; mated female behaviours

目前, 全世界离腹寡毛实蝇属 *Bactrocera* Macquart 实蝇有 651 种, 广泛分布于亚洲热带地区、南太平洋及澳大利亚, 其中经济上重要的实蝇害虫

有 50 多种, 且多具杂食性 (University of Hawaii, 2015; Vargas *et al.*, 2015)。在中国, 实蝇害虫主要来源于离腹寡毛实蝇属 *Bactrocera*, 严重危害了我国

基金项目: 国家自然科学基金项目(31760636); 云南生物资源保护与利用国家重点实验室开放基金(2015-004)

作者简介: 张秀歌, 女, 1989 年 1 月生, 河南汝州人, 博士研究生, 研究方向为昆虫化学生态学及害虫防治, E-mail: zxg19890113@163.com

* 通讯作者 Corresponding authors, E-mail: x.chun@163.com; dongwenxia@163.com

收稿日期 Received: 2017-06-23; 接受日期 Accepted: 2017-09-14

经济上重要的水果和蔬菜,例如芒果、桃、苹果、梨、柑橘、番石榴、牛油果、番茄、辣椒和瓜类等(Wan *et al.*, 2009; Liu *et al.*, 2013)。

目前,传统的杀虫剂化学防治、不育技术(sterile insect technique, SIT)、雄虫灭绝技术(male annihilation technique, MAT)是防控大多数实蝇的主要措施,但仍然在应用中存在不足之处(Daane and Johnson, 2010; Canale and Benelli, 2012; Lauzon and Potter, 2012; Beris *et al.*, 2013),急需新的环保型防控方法来防治实蝇。通过研究昆虫的求偶和交配行为有助于充分理解进化中的昆虫行为生态学,观察昆虫的交配系列行为有助于阐明配偶选择的评估方法和动态,从而建立基于昆虫行为的防治策略。因此,本文对离腹寡毛实蝇 *Bactrocera* spp. 两性的生殖通讯交流及相关的行为进行了概述。总结了雄虫在求偶炫耀场所同性斗争的特点,在求偶和交配期间影响配偶选择的物理、化学信号以及雌虫在产卵位置上的行为,包括产卵标记信息素(oviposition marking pheromones, OMPs)的利用和雌虫之间为单个产卵位置的竞争,并展望了将来的研究领域,以期实蝇害虫综合治理提供新的思路 and 参考。

1 实蝇的交配系统

实蝇中存在两个不同的一雄多雌制交配系统,即雄虫优势型一雄多雌制(male dominance polygyny)和资源保卫型一雄多雌制(resource defense polygyny)。在雄虫优势型一雄多雌制中,许多雄虫在求偶聚集场所(lekking sites)进行求偶炫耀(lek),并通过炫耀表演(leks)和攻击(aggression)等方式取得地位的竞争,获胜的雄虫在种群中占主导地位并与多头雌虫交配,而非优势雄虫则被排挤到求偶场所的边缘,从而失去交配的机会(Emlen and Oring, 1977);在资源保卫型一雄多雌制中,雄虫通过保卫雌虫繁殖所需的各种资源来间接控制雌虫。一般而言,虫体健壮的雄虫占据资源充裕的领域,而较弱的雄虫则退居到资源贫乏的区域中(Emlen and Oring, 1977)。

雄虫优势型一雄多雌制是许多热带、亚热带地区的杂食性的按实蝇属 *Anastrepha*、离腹寡毛实蝇属 *Bactrocera* 和腊实蝇属 *Ceratitis* 实蝇的典型交配系统,雄虫为交配的目的进行求偶炫耀(Kuba and Koyama, 1985; Arita and Kaneshiro, 1989; Whittier

et al., 1992; Benelli, 2014)。资源保卫型一雄多雌制是许多温带的专食性或寡食性实蝇的典型交配系统,尤其是绕实蝇属 *Rhagoletis* 的实蝇,雌虫需要雄虫通过雄虫间的斗争来保护资源(如产卵位置)(Opp *et al.*, 1996; Wilkinson and Johns, 2005)。通常,这些交配系统行为发生在每天或每年的不同时间和地点(Smith and Prokopy, 1980; Wilkinson and Johns, 2005)。

另外,也存在一些特殊的杂食性实蝇,其部分的交配行为属于专食性和寡食性实蝇特有的资源保卫型的交配系统(Headrick and Goeden, 1990)。如番木瓜实蝇 *Toxotrypana curvicauda* Gerstaecker 是一个典型的物种,具有较窄的寄主范围,产生性信息素但不发生求偶炫耀行为,其依靠了双交配系统(Landolt and Hendrichs, 1983)。同样地,另一个典型的实蝇 *Anastrepha robusta* Greene 雄虫也产生性信息素,但不进行求偶炫耀,仅在性信息素释放期间在寄主植物上持续性循环飞行且重复性降落(Aluja, 1993)。

2 实蝇雄成虫求偶交配行为

Aluja 和 Birke(1993)定义“lek”为至少 3 头求偶雄虫在非资源区域(通常在寄主和非寄主植物邻近水果的叶子上)的聚集性行为,其中每头雄虫占据领域表演求偶炫耀动作来吸引雌虫前来交配,并不依靠资源保卫型的交配系统(Höglund and Alatalo, 1995)。通常,求偶炫耀的雄虫通过释放作用于长距离范围的性信息素吸引雌虫到求偶场所,然后开始一系列的行为表现(Shelly, 2001)。对于雌虫来说,雌虫在求偶炫耀中的雄虫中选择表演行为(如雄虫翅的活动和嗅觉、触觉的信号等)最佳的雄虫进行交配(Kuba and Koyama, 1985; Benelli *et al.*, 2012a; Benelli, 2014),从而确保了雌虫的繁殖力、降低了干扰交配的风险、避免了天敌和减少了雌虫病害发生的可能性(Whittier and Kaneshiro, 1995; Shelly, 2000; Kumaran *et al.*, 2013),也间接确保了后代优良的遗传性状(Jones *et al.*, 1998)。然而,外界刺激信号是否调节了实蝇的求偶炫耀行为,目前还没有验证。但已有研究指出环境因素(如光强度、光周期)和雄虫发出的信号行为(如翅的动作、长距离信息素的释放)共同参与了对实蝇求偶炫耀行为的调节(Shelly, 2001; Quilici *et al.*, 2002; Segura *et al.*, 2007; Díaz-Fleischer and Arredondo, 2011)。

2.1 求偶炫耀的一系列行为

大多数的离腹寡毛实蝇属 *Bactrocera* 昆虫求偶炫耀系列行为可分为 3 个关键的阶段 (Perkins *et al.*, 1990a; Poramarcom and Boake, 1991)。首先, 雄虫为维护自己小的领域, 驱赶其它的雄虫, 然后产生性信息素嗅觉信号、翅振动的听觉信号以及视觉信号来吸引雌虫; 其次, 雌虫飞向雄虫, 降落并爬向雄虫; 最后, 雄虫感知到雌虫, 一次或多次尝试交配 (Koyama, 1989)。但橄榄实蝇 *B. oleae* (Rossi) 和柑橘大实蝇 *B. minax* (Enderlein) 的求偶交配行为稍稍不同于上述第一个阶段的求偶系列行为, 橄榄实蝇 *B. oleae* 雄虫首先为定位雌虫进行搜寻配偶的阶段, 然后通过听觉的信号做出求偶动作, 最后尝试交配 (Benelli *et al.*, 2012a), 柑橘大实蝇 *B. minax* 雄虫在第一阶段中没有求偶行为 (如翅振) (Dong *et al.*, 2014)。

营养交换行为 (mating trophallaxis) 也是实蝇求偶交配一系列行为的一部分, 一般发生在交配前、交配期间以及交配后, 持续时间很短。目前, 营养交换行为仅在 20 种实蝇中观察到, 在主要的实蝇害虫离

腹寡毛实蝇属 *Bactrocera* 中尚未发现 (Sivinski *et al.*, 2000)。

2.2 影响配偶选择的刺激信号

化学的、视觉的和听觉的刺激信号在昆虫两性间的通讯中占据重要作用。通常, 实蝇雄虫通过膨胀腹部外侧膜或挤压肛窝分泌性信息化合物 (Fitt, 1989), 然后通过展翅行为扩散这些信息素, 同时产生某种意义的声音 (Nufio and Papaj, 2001)。此外, 实蝇的体表通常色彩鲜艳, 或翅具有翅斑, 在配偶选择期间以特殊的方式来利用这些视觉信号。

2.2.1 性信息素化学信号: 性信息素在寻找配偶阶段占据重要作用。已有报道, 离腹寡毛实蝇属 *Bactrocera* 实蝇雄虫主要在直肠腺体产生性信息素来吸引雌虫 (表 1) (Tan *et al.*, 2014; El-Sayed, 2017)。其中至少 3 种实蝇, 瓜实蝇 *B. cucurbitae* (Baker and Bacon, 1985; Kuba and Sokei, 1988; Perkins *et al.*, 1990a)、橘小实蝇 *B. dorsalis* (Baker and Bacon, 1985; Perkins *et al.*, 1990b) 和橄榄实蝇 *B. oleae* (Canale *et al.*, 2013a) 雄虫和雌虫都可产生性信息素。

表 1 我国主要离腹寡毛实蝇属实蝇已鉴定的性信息素

Table 1 Sex pheromones identified from major *Bactrocera* species in China

实蝇 Species	性信息素 Sex pheromones	来源 Source	参考文献 References
番石榴实蝇 <i>B. correctae</i> (Bezzi)*	(Z)-松柏醇 (Z)-Coniferyl alcohol	雄虫直肠腺体 Male rectal gland	Tokushima <i>et al.</i> , 2010
	(Z)-3-(3,4-二甲氧基苯基)-2-丙烯-1-醇		
	(Z)-3,4-Dimethoxycinnamyl alcohol		
	β-石竹烯 β-Caryophyllene		
瓜实蝇 <i>B. cucurbitae</i> (Coquillet)	α-石竹烯 α-Caryophyllene	雌虫虫体顶空抽提 Aeration extracts from female	Baker and Bacon, 1985
	别香橙烯 Alloaromadendrene		
	对羟基苯甲酸乙酯 Ethyl 4-hydroxybenzoate		
	对羟基苯甲酸丙酯 Propyl 4-hydroxybenzoate		
	N-3-异戊基乙酰胺 N-3-Methylbutylacetamide		
	(E,E)-2,8-二甲基-1,7-二氧杂螺(5.5)十一烷		
	(E,E)-2,8-Dimethyl-1,7-dioxaspiro(5.5) undecane		
	(Z,E)-2,8-二甲基-1,7-二氧杂螺(5.5)十一烷		
	(Z,E)-2,8-Dimethyl-1,7-dioxaspiro(5.5) undecane		
	2,3,5,6-四甲基吡嗪 2,3,5,6-Tetramethylpyrazine		
2-甲基吡嗪 2-Methylpyrazine			
2,3,5-三甲基吡嗪 2,3,5-Trimethylpyrazine			
2-乙氧基苯甲酸 2-Ethoxybenzoic acid	雌虫虫体顶空抽提 Air collection from male	Ohinata <i>et al.</i> , 1982	
二十五烷 Pentacosane			
二十七烷 Heptacosane			
二十九烷 Nonacosane			
(E)-5-(3,6-庚二烯基)-二氢-2(3H)-呋喃酮	雌虫虫体顶空抽提 from male		
(E)-5-(3,6-heptadienyl)-dihydro-2(3H)-furanone			

续表 1 Table 1 continued

实蝇 Species	性信息素 Sex pheromones	来源 Source	参考文献 References
橘小实蝇 <i>B. dorsalis</i> (Hendel)	(<i>E, E</i>)-2-乙基-8-甲基-1,7-二氧杂螺(5.5)十一烷 (<i>E, E</i>)-2-Ethyl-8-methyl-1,7-dioxaspiro(5.5) undecane	雄虫直肠腺体 Male rectal gland	Perkins <i>et al.</i> , 1990b
	3-羟基-2,8-二甲基-1,7-二氧杂螺(5.5)十一烷 3-Hydroxy-2,8-dimethyl-1,7-dioxaspiro(5.5) undecane		
	丁二酸二甲酯 Dimethyl butanedioate		
	磷酸三甲酯 Trimethyl phosphate		
	<i>N</i> -3-甲基丁基乙酰胺 <i>N</i> -3-Methylbutylacetamide		
	2,3,5-三甲基吡嗪 2,3,5-Trimethylpyrazine		
	2-烯丙基-4,5-二甲氧基苯酚 2-Allyl-4,5-dimethoxyphenol		
	(<i>E</i>)-松柏醇(<i>E</i>)-Coniferyl alcohol		
	(<i>Z</i>)-3-(3,4-二甲氧基苯基)-2-丙烯-1-醇 (<i>Z</i>)-3,4-Dimethoxyphenyl-2-propen-1-ol		
	(<i>E, E</i>)-2,8-二甲基-1,7-二氧杂螺(5.5)十一烷 (<i>E, E</i>)-2,8-Dimethyl-1,7-dioxaspiro(5.5) undecane		
(<i>E, E</i>)-8-乙基-2-甲基-1,7-二氧杂螺(5.5)十一烷 (<i>E, E</i>)-8-Ethyl-2-methyl-1,7-dioxaspiro(5.5) undecane			
(<i>E, E</i>)-8-甲基-2-丙基-1,7-二氧杂螺(5.5)十一烷 (<i>E, E</i>)-8-Methyl-2-propyl-1,7-dioxaspiro(5.5) undecane			
<i>N</i> -2-甲基丁基丙酰胺 <i>N</i> -2-Methylbutylpropanamide			
(<i>E, E</i>)-2,8-二甲基-1,7-二氧杂螺(5.5)十一烷 (<i>E, E</i>)-2,8-Dimethyl-1,7-dioxaspiro(5.5) undecane	雌虫虫体顶空抽提 Air collection from male	Ohinata <i>et al.</i> , 1982	
(<i>E, Z</i>)-2,8-二甲基-1,7-二氧杂螺(5.5)十一烷 (<i>E, Z</i>)-2,8-Dimethyl-1,7-dioxaspiro(5.5) undecane			
6-氧-1-壬醇 6-oxo-Nonan-1-ol			
辣椒实蝇 <i>B. latifrons</i> (Hendel)	2-乙基-8-甲基-1,7-二氧杂螺(5.5)十一烷 2-Ethyl-8-methyl-1,7-dioxaspiro(5.5) undecane	雌虫腹部尖端 Female abdominal tips	Zhang <i>et al.</i> , 1997
	(2 <i>S</i> ,6 <i>R</i> ,8 <i>S</i>)-(<i>E, E</i>)-2,8-二甲基-1,7-二氧杂螺(5.5)十一烷 (2 <i>S</i> ,6 <i>R</i> ,8 <i>S</i>)-(<i>E, E</i>)-2,8-Dimethyl-1,7-dioxaspiro(5.5) undecane		
	2-异丙基-4,5-二甲基恶唑 2-Isopropyl-4,5-dimethyloxazole 2-仲丁基-4,5-二甲基恶唑 2-(1-Methylpropyl)-4,5-dimethyloxazole	雄虫直肠腺体 Male rectal gland	Avery <i>et al.</i> , 1996
柑橘大实蝇 <i>B. minax</i> (Enderlein) *	1,2-辛二醇 1,2-Octanediol 十六烷酸乙酯 Ethyl hexadecanoate	雄虫、雌虫直肠腺体 Male and female rectal gland	武可明, 2013; 周琼和刘路, 2013
南瓜实蝇 <i>B. tau</i> (Walker)	(<i>R</i>)-1,3-壬二醇(<i>R</i>)-Nonane-1,3-diol	雄虫直肠腺体 Male rectal gland	Perkins <i>et al.</i> , 1990a
	2-甲氧基- <i>N</i> -3-甲基丁基乙酰胺 2-Methoxy- <i>N</i> -3-methylbutylacetamide		
	<i>N</i> -3-甲基丁基乙酰胺 <i>N</i> -3-Methylbutylacetamide		

* 含有推测的性信息素 With the presumed sex pheromones.

2.2.2 听觉信号:早在 1954 年, Roan 等(1954)注意到橘小实蝇 *B. dorsalis* 产生的一种特有的高频嗡嗡声与黄昏时刻的交配行为有关。已报道, 实蝇雄虫通过翅振动和摩擦发声向雌虫发出求偶信号 (Keiser *et al.*, 1973; Benelli *et al.*, 2012a)。目前,

振翅和摩擦发声行为已在离腹寡毛实蝇属 *Bactrocera* 中经济上重要的瓜实蝇 *B. cucurbitae* (Kanmiya, 1988; Mir and Mir, 2016)、橘小实蝇 *B. dorsalis* (Poramarcom and Boake, 1991)、橄榄实蝇 *B. oleae* (Benelli *et al.*, 2012a) 中观察到。

首先,振翅行为在实蝇的求偶交配行为中具有重要的作用。Benelli 等(2014a)提到实蝇振翅行为作为交配刺激信号是为了试探雌虫交配的意愿。但也有研究表明,雄虫的振翅行为在求偶尝试阶段持续发生,是作为求偶的进一步行为表现,为抚慰雌虫(placate the female),也可能是为了在飞行定位配偶的过程中维持其自身平衡(Benelli *et al.*, 2012a)。对另一些离腹寡毛实蝇属 *Bactrocera* 实蝇而言,Keiser 等(1973)推断雄虫表现的振翅行为可能是为了在交配期间占据领域,但还没有研究可以证实这种说法。

其次,在许多节肢动物中,信号持续时间和脉冲重复频率作为雄虫适合度(fitness)的标志,对雌虫选择起重要作用(Parri *et al.*, 2002; Canale *et al.*, 2013b)。橄榄实蝇 *B. oleae* 雄虫翅振动的频率和脉冲持续时间影响雌虫在求偶期间的选择(Benelli *et al.*, 2012a)。在橘小实蝇 *B. dorsalis* 中,振翅动作时间长的雄虫交配成功率高,而时间短的雄虫很难吸引雌虫(Poramarcom and Boake, 1991)。

另外,在一些实蝇中,翅具有雌雄二型(wing sexual dimorphism)的特点,这是对听觉信号、嗅觉信号的一种适应性表现(Keiser *et al.*, 1973; Benelli *et al.*, 2012a)。例如,橄榄实蝇 *B. oleae* 雄虫的翅要比雌虫宽(Benelli *et al.*, 2012a),而且雄虫展开的翅后翼能够在振翅期间同时增强嗅觉信号的散发(Canale *et al.*, 2013a)。

2.2.3 视觉信号:视觉信号在昆虫两性通讯中的重要性是长期以来已经被公认的(Jang and Light, 1996; Dalby-Ball and Meats, 2000),但对于实蝇来说,其相关研究较少。

首先,实蝇翅具有的条带和斑点是视觉信号,雌雄二型上对一些实蝇的求偶和交配系列行为具有重要作用(Sivinski *et al.*, 2000)。其次,实蝇眼、足部的明亮颜色和图案在性行为中也可能具有通讯作用。实蝇 *Eutreta diana* (Osten Sacken) 雄虫在求偶期间举起腿节的中部,其颜色为黑色夹杂黄色小点(Sivinski *et al.*, 2000)。再者,雄虫的一些其他结构也具有视觉信号的作用,如鹿角实蝇 *Phytalmia* spp. 的雄虫头部形似鹿角的结构,实蝇 *Chetostoma curvinerve* Rondani 头部的一排扩展的刚毛,实蝇 *Stemonocora cornuta* (Scopoli) 头部额上向前突出的部分,实蝇 *Cerajocera ceratocera* Hendelthe 触角上突出的像毛状号角的梗节,实蝇 *Euphranta maculifemur* (Meijere) 胸足上宽且凹形的前基跗节,腊实蝇

Ceratitis spp. 足的胫节、腿节附着的长的刚毛,实蝇 *Trupanea bruneipennis* Hardy 腹部第五节背板大量的微黄色刚毛。在离腹寡毛实蝇属 *Bactrocera* spp. 中,大多实蝇不具独特的翅斑和条带,因此和其它实蝇相比,特有的翅动作很少(Sivinski *et al.*, 2000)。目前,这些视觉信号在求偶交配行为中的作用还没被研究证明,需进一步的深入研究。

2.2.4 影响实蝇交配行为的其他因素:实蝇昆虫的求偶交配行为也受环境的(Díaz Fleischer and Arredondo, 2011)、生态的(Leftwich *et al.*, 2012)、生理学的(Gavriel *et al.*, 2009; Anjos-Duarte *et al.*, 2011; Pérez-Staples *et al.*, 2012; Shelly *et al.*, 2012)和形态学的(Miranda, 2000; Harwood *et al.*, 2013)因素等的影响。

首先,低的光强度能增强橄榄实蝇 *B. oleae* 在水果周围的交配成功率(Kokkari *et al.*, 未发表数据);具有丰富蛋白质的饲料能够增强雄虫与雌虫交配的能力(Pereira *et al.*, 2012; Pérez-Staples *et al.*, 2012)。其次,橄榄实蝇 *B. oleae* 消化道中的细菌有助于提高以饲料喂养的成虫适合度(Ben-Yosef *et al.*, 2010)。再者,雌虫的交配选择随着日龄的不同而变化,从而影响雌虫选择雄虫的可能性(Pérez-Staples *et al.*, 2012)。另外,在大量饲养的拥挤条件下,密度效应影响雄虫的求偶行为,进而影响交配成功率(Benelli *et al.*, 2014a)。

形态学因素也影响交配行为,研究表明雄虫个体大小影响雄虫繁育后代。在橄榄实蝇 *B. oleae* 和昆士兰实蝇 *B. tryoni* (Froggatt) 中,较大个体的雄虫的成功交配比较小个体的更为容易(Benelli *et al.*, 2014a, 2016; Ekanayake *et al.*, 2017)。最有可能的原因是较大的雄虫能够产生较高质量的听觉信号如振翅和摩擦发声、高频求偶信号、短脉冲音程或者嗡嗡声(Benelli *et al.*, 2016),也有可能是大个体的雄虫具有超强的战斗能力(Benelli, 2014),或是克服雌虫阻力的能力(Taylor and Yuval, 1999)。

另外,类信息素(parapheromones)的化学物质,如甲基丁香酚(ME)、诱蝇酮(CL)、覆盆子酮(RK)等,从生理学和行为方面影响实蝇的生殖通讯系统(Renou and Guerrero, 2000)。实蝇雄成虫取食ME, CL和RK诱剂后,交配成功率、交配性能、性选择、交配竞争力显著提高(Shelly, 2010; Kumaran *et al.*, 2013, 2014a, 2014b; Wee *et al.*, 2017)。雌、雄的成功交配也可能受其他的触觉信号(低挥发性的表皮碳氢化合物)所影响,特别是雄虫通过足部摩

擦雌虫的腹部来感知信号 (Benelli *et al.*, 2014a)。

2.3 实蝇求偶炫耀场所

实蝇求偶炫耀的场所焦点位置,在这里雄虫之间为雌虫竞争(同性间选择)以及雌虫对雄虫的有效选择(两性间的选择) (Fiske *et al.*, 1998)。在交配系统为雄虫优势型一雄多雌制的实蝇中,不同的离腹寡毛实蝇属 *Bactrocera* 实蝇求偶炫耀场所不同。求偶炫耀场所可能在实蝇寄主植物的不同部分,也可能在远离寄主植物的地方 (Aluja and Norrbom, 1999)。橄榄实蝇 *B. oleae* 雄虫偏好在橄榄树迎风面进行雄虫间的攻击行为,在橄榄叶上进行交配行为 (Benelli, 2014)。瓜实蝇 *B. cucurbitae* 雄虫主要聚集在非寄主树木或杂草周围,并降落在树叶或杂草的下表面摩擦翅、释放信息素,并排斥其它的雄虫接近,在周围形成了小片的领域,从而引诱雌虫到这里 (Kuba and Koyama, 1985; Koyama *et al.*, 2004; Mir and Mir, 2016)。在交配系统以资源保卫型一雄多雌制的绕实蝇 *Rhagoletis* spp. 中,雄虫虽不发生求偶炫耀行为,但雄虫通常在樱桃果的周围聚集、争斗,部分实蝇也可发生在寄主植物叶片上 (Smith and Prokopy, 1980, 1982; Messina and Subler, 1995)。

实蝇的求偶炫耀位置也受环境因素的影响。Tychsen (1978) 指出风向影响昆士兰实蝇 *B. tryoni* 在寄主植物上的求偶炫耀位置。杨桃实蝇 *B. cacuminata* (Hering) 对交配位置的选择可能受特定的因素如光强度、高度和食物量的影响 (Raghu *et al.*, 2004)。

实蝇的求偶炫耀行为不同于脊椎动物 (Widemo and Owens, 1999)。实蝇的求偶炫耀场所具有短暂性 (Shelly and Kaneshiro, 1991), 雄虫在同性竞争时能够避免彼此严重伤害,个体对场所独占性不强 (low site fidelity), 这可能与实蝇在有限环境内单位面积上的高飞行密度有关 (Benelli, 2014)。在野外条件下,实蝇雄虫通常可以维持求偶场所时间很久,以获得更多的竞争成功。因此,野外的研究还需进一步深入。

2.4 实蝇雄成虫的攻击性行为

雄虫间的攻击性行为在两个交配系统中均有发生,其特点是挥翅、头部对接、前足相互搏击,如入侵实蝇 *B. invadens* Drew, Tsuruta & White (Ekesi *et al.*, 2009)、橄榄实蝇 *B. oleae* (Benelli, 2014)、瓜实蝇 *B. cucurbitae* (Kuba and Koyama, 1985; Koyama *et al.*, 2004; Mir and Mir, 2016),但是这一系列的

行为之间的相互关系还尚未清楚。相比之下,其它实蝇在雄虫争斗期间的一系列行为是简单的,例如橘小实蝇 *B. dorsalis* 雄虫仅仅飞向另一雄虫,驱赶其离开叶子,而不存在头部对接撞击的行为 (Shelly and Kaneshiro, 1991)。实蝇 *Paracantha gentilis* 雄虫的攻击行为表现为翅的挥动、追逐和头部对撞,而不存在前足相互搏击 (Headrick and Goeden, 1994)。

雄虫的攻击性行为一般在何时发生呢? 目前,有关雄虫攻击行为的昼夜动态还未有详细的研究。大部分的攻击行为观察是伴随着求偶和交配的行为研究。其中对离腹寡毛实蝇 *Bactrocera* 的攻击行为研究较少。橄榄实蝇 *B. oleae* 在将近正午和下午时发生攻击行为,但在将近正午时比在下午时发生斗争行为的虫数更多,平均持续时间更久 (Benelli, 2014),橘小实蝇 *B. dorsalis* 在黄昏前 2-3 h 发生 (Shelly and Kaneshiro, 1991),瓜实蝇 *B. cucurbitae* 的攻击行为发生在近黄昏时候 (Kuba and Koyama, 1985)。

近来,也有研究报道了实蝇的攻击行为具有偏侧性 (lateralization) (Benelli *et al.*, 2015a; Benelli, 2015b),但在实蝇中非常少见。如地中海实蝇 *C. capitata* (Wiedemann) 表现攻击行为时左侧的翅、足比右侧的快(翅的击打和足的搏击行为),橄榄实蝇 *B. oleae* 在利用身体左侧部分攻击时,争斗的成功率更高,表现出偏左的群体偏侧性 (Benelli *et al.*, 2015a, 2015b)。据推测实蝇的群体水平的攻击行为偏侧性可能与雄虫为交配以及雌虫为产卵位置竞争的长期的社会互动性行为有关 (Benelli *et al.*, 2015a, 2015b)。攻击争斗行为的偏侧性有利于充分阐释昆虫的进化生态学,但是否已在多个实蝇种中存在以及其适合度是否高于其他非偏侧性的实蝇,还需要进一步的研究。

3 交配后实蝇雌成虫行为

目前的理论认为,实蝇雌虫依靠两种行为方法,如产卵标记信息素 (OMPs) 的利用和产卵位置上雌虫间的竞争行为来维护产卵位置,从而增加后代生长发育的成功率 (Benelli *et al.*, 2014a, 2014b; Benelli, 2015a, 2015b)。

由于有限的食物源,同种的雌虫在识别 OMPs 后,可避免在已标记位置上产卵。在离腹寡毛实蝇属 *Bactrocera* 中,瓜实蝇 *B. cucurbitae*、橘小实蝇 *B. dorsalis*、昆士兰实蝇 *B. tryoni* 和扎维斯实蝇 *B.*

jarvisi (Tryon) 在产卵后取下产卵器, 没有发现产卵标记信息素 (Prokopy and Koyama, 1982; Fitt, 1984; Prokopy *et al.*, 1989), 但是在橄榄实蝇 *B. oleae* 中观察到雌虫产卵后, 口器唇瓣在水果表皮散布产卵孔溢出的橄榄汁抑制了其它雌虫的产卵 (Girolami *et al.*, 1981), 表明其可能存在 OMPs。通常, 同种间雌虫对 OMPs 的不同行为反应表现为抑制产卵行为 (Averill and Prokopy, 1989)、干扰产卵行为 (Papaj *et al.*, 1989, 1992)、迁出实蝇高发区 (Roitberg *et al.*, 1982, 1984) 以及降低产卵量 (Papaj *et al.*, 1989, 1990)。

雌虫产卵位置上的竞争行为, 在大多实蝇中普遍存在, 如橘小实蝇 *B. dorsalis* (Shelly, 1999)、入侵实蝇 *B. invadens* (Ekesi *et al.*, 2009)、橄榄实蝇 *B. oleae* (Benelli, 2014)、昆士兰实蝇 *B. tryoni* (Pritchard, 1969) 等, 其雌虫间的竞争包含攻击性行为, 类似于在雄虫间观察到的攻击性行为, 基本上包括翅的挥动、追逐、猛扑和前足搏击动作 (Headrick and Goeden, 1990; Benelli *et al.*, 2014a)。实蝇雌虫不仅在同种个体间存在竞争行为, 在异种个体间也可通过竞争行为 (翅挥动、猛扑和前足搏击动作) 抵御其它节肢动物 (寄生蜂等), 如橘小实蝇 *B. dorsalis* 在产卵后防止阿里山潜蝇茧蜂 *Fopius arisanus* (Sonan) (Messing, 私人通讯) 寄生 (Benelli, 2015a); 橄榄实蝇 *B. oleae* 为维护产卵位置防御短背茧蜂 *Psytalia concolor* Szépligeti (Benelli and Canale, 2016); 入侵果实蝇 *B. invadens* 阻止非洲芒果实蝇 *C. cosyra* (Walker) 取食同一寄主植物芒果 (Ekesi *et al.*, 2009)。但是, 为充分揭示异种个体间的相互关系, 需要进一步研究寄生蜂对实蝇攻击性行为的反应。

与雄虫不同, 雌虫间的争斗行为大多发生在寄主植物叶片上及室内饲养笼的壁上 (Briceño *et al.*, 1999; Benelli, 2014), 但对于橄榄实蝇 *B. oleae* 来说, 其发生在寄主植物水果橄榄上 (Benelli, 2014)。和橄榄实蝇 *B. oleae* 雄虫一样, 雌虫的攻击斗争行为发生在将近正午时和下午时, 且在将近正午时发生攻击行为的虫数比下午时的高, 但其斗争持续时间在两个时间段内没有差异 (Benelli, 2014)。

4 小结与展望

目前, 有关实蝇特别是实蝇复合种的生态、行为学研究较少。因此, 有必要在制定防治策略之前, 充

分理解其生态和行为学。已有大量的文献报道了实蝇的监测和管理方法, 包括雄虫不育和灭绝技术、大量诱捕法、化学诱剂、交配干扰法和生物防治法 (Ansari *et al.*, 2012; Shelly *et al.*, 2014; Vargas *et al.*, 2015)。但是使用者仅使用其中防治效果较为满意的极少数方法, 而其他方法由于缺少实蝇生态学、行为学知识, 防治效果不好, 不容易被采用。如果将有关的种群动态、行为学和其他相关的生态因子方面的信息联系在一起, 并在正确的时间和地点制定出适当的害虫防治方法, 将为未来实蝇的生态的、行为学的研究及防治奠定基础, 从而探索出成功的、可靠的害虫防治策略 (Ansari *et al.*, 2012)。

首先, 通过行为学和化学生态学的研究, 昆虫不育技术 (SIT) 在国外已经被广泛用于防治地中海实蝇 *C. capitata*、墨西哥按实蝇 *A. ludens* (Loew)、橘小实蝇 *B. dorsalis*、瓜实蝇 *B. cucurbitae* 和橄榄实蝇 *B. oleae*, 已取得显著的防治效果 (Ant *et al.*, 2012; Yuval *et al.*, 2013)。目前, 在我国, 利用 SIT 技术防治橘小实蝇 *B. dorsalis* (季清娥等, 2007a, 2007b, 2008; 洪静芳等, 2014)、柑橘大实蝇 *B. minax* 已取得了初步成效 (王金涛等, 2013), 但仍有很多工作尚需进一步研究和探索。

其次, 研究实蝇攻击性行为的变化, 有助于认识实蝇生理学的、生态学的及进化的问题, 也利于提高田间的实际应用, 因此需要对此进行更深度的观察。目前, 有关雄虫间攻击性行为的昼夜周期性变化、引起攻击行为的信号、先前经历对行为表现的作用以及攻击行为的偏侧性演化研究少之又少, 值得进一步的研究。

然后, 实蝇性信息素混合物能提高检测和大量诱捕实蝇的效果 (Gil-Ortiz, 2015)。当其他的 IPM 技术方法不实用或效果不好, 其就显得尤为重要 (Daane and Johnson, 2010; Benelli and Canale, 2012; Benelli *et al.*, 2013a)。但目前, 实蝇性信息素的研究仍存在一些问题: (1) 具有多组分成分, 每个组分具有复杂的化学结构, 合成成本高, 与雄虫引诱剂和食物诱剂相比诱捕效果低; (2) 田间使用时易受非生物因素的影响 (最佳混配试剂的化学稳定性变化、蒸汽压力变化及其释放速率等); (3) 嗅觉信号相对于物理信号 (视觉的、听觉的信号等) 是否对实蝇的交配行为产生了十分重要的影响。这些都在一定程度上限制了性信息素在实蝇诱捕和防治上的应用。而且, 雄虫诱剂, 特别是甲基丁香酚 (ME)、诱蝇酮/覆盆子酮 (CL/RK) 虽已经普遍用于

离腹寡毛实蝇属 *Bactrocera* 实蝇的诱捕和防治,但有研究认为 ME 具有致癌性 (Sekizawa and Shibamoto, 1982; Schiestl *et al.*, 1989; Zhou *et al.*, 2007), 而 CL/RK 较 ME 挥发性低、诱捕效果差 (Tan *et al.*, 2014), 也需要研究一种替代的化合物。因此, 将来的研究目标应该从以下 4 个方面来实现。首先, 实蝇性信息素的研究; 其次, 天然的小分子物质代替有毒化合物, 使实蝇害虫摄入并接触, 发挥其毒性 (Piñero *et al.*, 2011; Benelli *et al.*, 2012b; Canale *et al.*, 2013b; Piñero *et al.*, 2013), 但对非靶标节肢动物低毒 (Benelli *et al.*, 2013b); 然后, 研究不需要杀虫剂的诱捕器 (Vargas *et al.*, 2010)。最后, 深入进行实蝇有关行为生态学和化学生态学的观察和研究, 以利于提高诱剂诱捕效果, 如 Koyama 等 (2004) 在瓜实蝇 *B. cucurbitae* 求偶炫耀场所释放诱剂。

最后, 由于对传粉者蜜蜂、食蚜虻等及寄生蜂有益的特点, 产卵标记信息素为实蝇害虫综合治理提供了对生态环境友好的策略 (Arredondo and Díaz-Fleischer, 2006; Aluja *et al.*, 2009), 同样是防治实蝇主要的手段。目前, 此方法已成功应用于橄榄实蝇 *B. oleae* 上, 通过寄生蜂感知 OMPs 来进行生物防治 (Daane and Johnson, 2010; Benelli and Canale, 2012; Benelli *et al.*, 2013b)。但是在其它经济上重要的实蝇上, OMPs 的存在及作用还没有更多的研究。另外, 由于寄生蜂具有对寄主信号学习和经验行为的特点, 从而加快了寄主搜寻、定位 (Canale and Benelli, 2012; Ngumbi *et al.*, 2012), 因此在释放实蝇寄生蜂之前利用 OMPs 对其驯化, 使之敏感, 有利于提高寄生蜂在田间的寄生能力。因此, OMPs 的合成及生物防治方法也是将来实蝇的一个研究方向。

参考文献 (References)

- Aluja M, 1993. Unusual calling behavior of *Anastrepha robusta* (Diptera: Tephritidae) flies in nature. *Fla. Entomol.*, 76(2): 391–395.
- Aluja M, Birke A, 1993. Habitat use by adults of *Anastrepha obliqua*flies (Diptera: Tephritidae) in a mixed mango and tropical plum orchard. *Ann. Entomol. Soc. Am.*, 86(6): 799–812.
- Aluja M, Diaz-Fleischer F, Boller EF, Hurter J, Edmunds AJF, Hagmann L, Patrian B, Reyes J, 2009. Application of feces extracts and synthetic analogues of the host marking pheromone of *Anastrepha ludens* significantly reduces fruit infestation by *A. obliqua* in tropical plum and mango backyard orchards. *J. Econ. Entomol.*, 102(6): 2268–2278.
- Aluja M, Norrbom AL, 1999. Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior. CRC Press: Boca Raton, FL, USA.
- Anjos-Duarte CS, Moreira Costa A, Joachim-Bravo IS, 2011. Influence of female age on variation of mate choice behavior in Mediterranean fruit fly (Diptera: Tephritidae). *J. Insect Behav.*, 24(1): 11–21.
- Ansari MS, Hasan F, Ahmad N, 2012. Threats to fruit and vegetable crops: fruit flies (Tephritidae) – ecology, behaviour, and management. *J. Crop Sci. Biotechnol.*, 15(3): 169–188.
- Ant T, Koukidou M, Rempoulakis P, Gong HF, Economopoulos A, Vontas J, Alphey L, 2012. Control of the olive fruit fly using genetics-enhanced sterile insect technique. *BMC Biol.*, 10: 51.
- Arita LH, Kaneshiro KY, 1989. Sexual selection and lek behavior in the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae). *Pac. Sci.*, 43(2): 135–143.
- Arredondo J, Diaz-Fleischer F, 2006. Oviposition deterrents for the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae) from fly faeces extracts. *Bull. Entomol. Res.*, 96(1): 35–42.
- Averill AL, Prokopy RJ, 1989. Host-marking pheromones. In: Robinson AS, Hooper G eds. Fruit Flies: Their Biology, Natural Enemies and Control. Elsevier, Amsterdam. 207–219.
- Avery JW, Liquido N, Cunningham RT, Leonhardt BA, Waters ILM, 1996. Volatile components of rectal glands of the Malaysian fruit fly *Bactrocera latifrons* (Diptera: Tephritidae). *J. Am. Chem. Soc.*, 211: 102.
- Baker R, Bacon AJ, 1985. The identification of spiroacetals in the volatile secretions of two species of fruit fly (*Dacus dorsalis*, *Dacus cucurbitae*). *Experientia*, 41(11): 1484–1485.
- Baker R, Herbert RH, Lomer RA, 1982. Chemical components of the rectal gland secretions of male *Dacus cucurbitae*, the melon fly. *Experientia*, 38(2): 232–233.
- Benelli G, 2014. Aggressive behavior and territoriality in the olive fruit fly, *Bactrocera oleae* (Rossi) (Diptera: Tephritidae): role of residence and time of day. *J. Insect Behav.*, 27(2): 145–161.
- Benelli G, 2015a. Should I fight or should I flight? How studying insect aggression can help integrated pest management. *Pest Manag. Sci.*, 71(7): 885–892.
- Benelli G, 2015b. Aggression in Tephritidae flies: where, when, why? Future directions for research in integrated pest management. *Insects*, 6(1): 38–53.
- Benelli G, Canale A, 2012. Learning of visual cues in the fruit fly parasitoid *Psytalia concolor* (Szépligeti) (Hymenoptera: Braconidae). *BioControl*, 57(6): 767–777.
- Benelli G, Canale A, 2016. Aggressive behavior in olive fruit fly females: oviposition site guarding against parasitic wasps. *J. Insect Behav.*, 29(6): 680–688.
- Benelli G, Canale A, Bonsignori G, Ragni G, Stefanini C, Raspi A, 2012a. Male wing vibration in the mating behavior of the olive fruit fly *Bactrocera oleae* (Rossi) (Diptera: Tephritidae). *J. Insect Behav.*, 25(6): 590–603.
- Benelli G, Canale A, Flamini G, Cioni PL, Demi F, Ceccarini L, Macchia M, Conti B, 2013a. Biototoxicity of *Melaleuca alternifolia* (Myrtaceae) essential oil against the Mediterranean fruit fly,

- Ceratitis capitata* (Diptera: Tephritidae), and its parasitoid *Psytalia concolor* (Hymenoptera: Braconidae). *Ind. Crops Prod.*, 50: 596–603.
- Benelli G, Daane KM, Canale A, Niu CY, Messing RH, Vargas RI, 2014a. Sexual communication and related behaviours in Tephritidae: current knowledge and potential applications for Integrated Pest Management. *J. Pest Sci.*, 87(3): 385–405.
- Benelli G, Donati E, Romano D, Ragni G, Bonsignori G, Stefanini C, Canale A, 2016. Is bigger better? Male body size affects wing-borne courtship signals and mating success in the olive fruit fly, *Bactrocera oleae* (Diptera: Tephritidae). *Insect Sci.*, 23(6): 869–880.
- Benelli G, Donati E, Romano D, Stefanini C, Messing RH, Canale A, 2015a. Lateralisation of aggressive displays in a tephritid fly. *Sci. Nat.*, 102(1–2): 1–9.
- Benelli G, Flamini G, Canale A, Cioni PL, Conti B, 2012b. Toxicity of some essential oil formulations against the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) (Diptera Tephritidae). *Crop Prot.*, 42: 223–229.
- Benelli G, Giunti G, Canale A, Messing RH, 2014b. Lek dynamics and cues evoking mating behavior in tephritid flies infesting soft fruits: implications for behavior-based control tools. *Appl. Entomol. Zool.*, 49(3): 363–373.
- Benelli G, Revadi S, Carpita A, Giunti G, Raspi A, Anfora G, Canale A, 2013b. Behavioral and electrophysiological responses of the parasitic wasp *Psytalia concolor* (Szépligeti) (Hymenoptera: Braconidae) to *Ceratitis capitata*-induced fruit volatiles. *Biol. Control.*, 64(2): 116–124.
- Benelli G, Romano D, Messing RH, Canale A, 2015b. Population-level lateralized aggressive and courtship displays make better fighters not lovers: evidence from a fly. *Behav. Process.*, 115: 163–168.
- Ben-Yosef M, Aharon Y, Jurkevitch E, Yuval B, 2010. Give us the tools and we will do the job; symbiotic bacteria affect olive fly fitness in a diet-dependent fashion. *Proc. R. Soc. B*, 277(1687): 1545–1552.
- Beris EI, Papachristos DP, Fytrou A, Antonatos SA, Kontodimas DC, 2013. Pathogenicity of three entomopathogenic fungi on pupae and adults of the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae). *J. Pest. Sci.*, 86(2): 275–284.
- Briceño RD, Ramos D, Eberhard WG, 1999. Aggressive behavior in medflies (*Ceratitis capitata*) and its modification by mass rearing (Diptera: Tephritidae). *J. Kans. Entomol. Soc.*, 72(1): 17–27.
- Canale A, Benelli G, 2012. Impact of mass-rearing on the host-seeking behaviour and parasitism by the fruit fly parasitoid *Psytalia concolor* (Szépligeti) (Hymenoptera: Braconidae). *J. Pest Sci.*, 85(1): 65–74.
- Canale A, Benelli G, Lanzo F, Giannotti P, Mazzoni V, Lucchi A, 2013b. The courtship song of fanning males in the fruit fly parasitoid *Psytalia concolor* (Szépligeti) (Hymenoptera: Braconidae). *Bull. Entomol. Res.*, 103(3): 303–309.
- Canale A, Germinara SG, Carpita A, Benelli G, Bonsignori G, Stefanini C, Raspi A, Rotundo G, 2013a. Behavioural and electrophysiological responses of the olive fruit fly, *Bactrocera oleae* (Rossi) (Diptera: Tephritidae), to male- and female-borne sex attractants. *Chemoecology*, 23(3): 155–164.
- Daane KM, Johnson MW, 2010. Olive fruit fly: managing an ancient pest in modern times. *Annu. Rev. Entomol.*, 55: 151–169.
- Dalby-Ball G, Meats A, 2000. Effect of fruit abundance within a tree canopy on the behaviour of wild and cultured Queensland fruit-fly *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). *Aust. J. Entomol.*, 39(3): 201–207.
- Diaz-Fleischer F, Arredondo J, 2011. Light conditions affect sexual performance in a lekking tephritid fruit fly. *J. Exp. Biol.*, 214(15): 2595–2602.
- Dong YC, Wan L, Pereira R, Desneux N, Niu CY, 2014. Feeding and mating behaviour of Chinese citrus fly *Bactrocera minax* (Diptera, Tephritidae) in the field. *J. Pest Sci.*, 87(10): 647–657.
- Ekanayake EWMTD, Clarke AR, Schutze MK, 2017. Effect of body size, age, and premating experience on male mating success in *Bactrocera tryoni* (Diptera: Tephritidae). *J. Econ. Entomol.*, 110(5): 2278–2281.
- Ekesi S, Billah MK, Peterson W, Nderitu W, Lux SA, Rwomushana I, 2009. Evidence for competitive displacement of *Ceratitis cosyra* by the invasive fruit fly *Bactrocera invadens* (Diptera: Tephritidae) on mango and mechanisms contributing to the displacement. *J. Econ. Entomol.*, 102(3): 981–991.
- El-Sayed AM, 2017. The Pherobase: Database of Insect Pheromones and Semiochemicals. <http://www.pherobase.com>. [accessed on 26 May 2017]
- Emlen ST, Oring LW, 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, 197(4300): 215–223.
- Fiske P, Rintamäki PT, Karvonen E, 1998. Mating success in lekking males: a meta-analysis. *Behav. Ecol.*, 9(4): 328–338.
- Fitt GP, 1984. Oviposition behaviour of two tephritid fruit flies, *Dacus tryoni* and *Dacus jarvisi*, as influenced by the presence of larvae in the host fruit. *Oecologia*, 62(1): 37–46.
- Fitt GP, 1989. The role of interspecific interactions in the dynamics of tephritid populations. In: Robinson AS, Hooper G eds. *Fruit Flies: Their Biology, Natural Enemies and Control*. World Crop Pests, Elsevier, Amsterdam. 281–300.
- Gavriel S, Gazit Y, Yuval B, 2009. Remating by female Mediterranean fruit flies (*Ceratitis capitata*, Diptera: Tephritidae): temporal patterns and modulation by male condition. *J. Insect Physiol.*, 55(7): 637–642.
- Gil-Ortiz R, 2015. Development of new ecological long-lasting dispensers of semiochemicals for the control of *Bactrocera oleae* (Rossi). *Pest Manag. Sci.*, 71(12): 1685–1693.
- Girolami V, Vianello A, Strapazzon A, Ragazzi E, Veronese G, 1981. Ovipositional deterrents in *Dacus oleae*. *Entomol. Exp. Appl.*, 29(2): 177–188.
- Harwood JF, Vargas RI, Care JR, 2013. Leg impairment magnifies reproductive costs in male Mediterranean fruit flies, *Ceratitis capitata*. *Entomol. Exp. Appl.*, 147(1): 73–81.
- Headrick D, Goeden RD, 1990. Life history of *Paracantha gentilis*

- (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.*, 83(4): 776 – 785.
- Headrick DH, Goeden RD, 1994. Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera) mating systems. *Stud. Dipterol.*, 1: 194 – 252.
- Höglund J, Alatalo R, 1995. Leks. Princeton University Press, Princeton.
- Hong JF, Ji QE, Chen JH, 2014. Effects of irradiated eggs on development and reproduction of *Bactrocera dorsalis* (Hendel). *J. Nucl. Agric. Sci.*, 28(3): 418 – 422. [洪静芳, 季清娥, 陈家骅, 2014. 卵期辐照对橘小实蝇生长发育繁殖的影响. *核农学报*, 28(3): 418 – 422]
- Jang EB, Light DM, 1996. Olfactory semiochemicals of tephritids. In: McPheron BA, Steck GS eds. *Fruit Fly Pests: A World Assessment of their Biology and Management*. St. Lucie Press, Delray Beach. 73 – 90.
- Ji QE, Du YG, Hou WR, Chen JH, 2008. Viability of the miss-sexed female pupae in the process of application of sterile insect technique of male Oriental fruit fly, *Bactrocera dorsalis* (Hendel). *J. Nucl. Agric. Sci.*, 22(1): 97 – 100. [季清娥, 杜迎刚, 侯伟荣, 陈家骅, 2008. 橘小实蝇雄性不育技术应用过程中混入雌虫活力的研究. *核农学报*, 22(1): 97 – 100]
- Ji QE, Hou WR, Chen JH, 2007a. Sterile insect technique of oriental fruit fly, *Bactrocera dorsalis* (Hendel) – optimal pupal age and dose of irradiation treatment for male pupae. *J. Nucl. Agric. Sci.*, 21(5): 523 – 526. [季清娥, 侯伟荣, 陈家骅, 2007a. 橘小实蝇雄性不育技术——雄蛹辐照最佳时期和剂量. *核农学报*, 21(5): 523 – 526]
- Ji QE, Hou WR, Chen JH, 2007b. Development of a genetic sexing strain and the sterile male technique of the Oriental fruit fly, *Bactrocera dorsalis* (Hendel). *Acta Entomol. Sin.*, 50(10): 1002 – 1008. [季清娥, 侯伟荣, 陈家骅, 2007b. 橘小实蝇遗传性别品系的建立及雄性不育技术. *昆虫学报*, 50(10): 1002 – 1008]
- Jones TM, Quinnell RJ, Balmford A, 1998. Fisherian flies: benefits of female choice in a lekking sandfly. *Proc. R. Soc. B*, 265(1406): 1651 – 1657.
- Kanmiya K, 1988. Acoustic studies on the mechanism of sound production in the mating songs of the melon fly, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae). *J. Ethol.*, 6(2): 143 – 151.
- Keiser I, Kobayashi RM, Chambers DL, Schneider EL, 1973. Relation of sexual dimorphism in the wings, potential stridulation, and illumination to mating of oriental fruit flies, melon flies, and Mediterranean fruit flies in Hawaii. *Ann. Entomol. Soc. Am.*, 66(5): 937 – 941.
- Kitching W, Lewis JA, Fletcher MT, Drew RAI, Moore CJ, Francke W, 1986. Spiroacetals in rectal gland secretions of Australasian fruit fly species. *J. Chem. Soc. Chem. Commun.*, 11: 853 – 854.
- Koyama J, 1989. Mating pheromones. Tropical dacines. In: Robinson AS, Hooper G eds. *Fruit Flies: Their Biology, Natural Enemies and Control*, vol 3A. Elsevier, Amsterdam. 165 – 168.
- Koyama J, Kakinohana H, Miyatake T, 2004. Eradication of the melon fly, *Bactrocera cucurbitae*, in Japan: importance of behavior, ecology, genetics, and evolution. *Annu. Rev. Entomol.*, 49(1): 331 – 349.
- Kuba H, Koyama J, 1985. Mating behavior of wild melon flies, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae) in a field cage: courtship behavior. *Appl. Entomol. Zool.*, 20(4): 365 – 372.
- Kuba H, Sokei Y, 1988. The production of pheromone clouds by spraying in the melon fly, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae). *J. Ethol.*, 6(2): 105 – 110.
- Kumaran NK, Balagawi S, Schutze M, Clarke AR, 2013. Evolution of lure response in tephritid fruit flies: phytochemicals as drivers of sexual selection. *Anim. Behav.*, 85(4): 781 – 789.
- Kumaran NK, Hayes RA, Clarke AR, 2014b. Cuelure but not zingerone make the sex pheromone of male *Bactrocera tryoni* (Tephritidae: Diptera) more attractive to females. *J. Insect Physiol.*, 68: 36 – 43.
- Kumaran NK, Prentis P, Mangalam KP, Schutze MK, Clarke AR, 2014a. Sexual selection in true fruit flies (Diptera: Tephritidae): transcriptome and experimental evidences for phytochemicals increasing male competitive ability. *Mol. Ecol.*, 23(18): 4645 – 4657.
- Landolt PJ, Hendrichs J, 1983. Reproductive behavior of the papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.*, 76(3): 413 – 417.
- Lauzon CR, Potter SE, 2012. Description of the irradiated and nonirradiated midgut of *Ceratitis capitata* Wiedemann (Diptera: Tephritidae) and *Anastrepha ludens* Loew (Diptera: Tephritidae) used for sterile insect technique. *J. Pest Sci.*, 85(2): 217 – 226.
- Leftwich PT, Edward DA, Alphey L, Gage MJG, Chapman T, 2012. Variation in adult sex ratio alters the association between courtship, mating frequency and paternity in the lek-forming fruit fly *Ceratitis capitata*. *J. Evol. Biol.*, 25(9): 1732 – 1740.
- Liu X, Jin Y, Ye H, 2013. Recent spread and climatic ecological niche of the invasive guava fruit fly, *Bactrocera correcta*, in mainland China. *J. Pest Sci.*, 86(3): 449 – 458.
- Messina FJ, Subler JK, 1995. Conspecific and heterospecific interactions of male *Rhagoletis* flies (Diptera: Tephritidae) on a shared host. *J. Kans. Entomol. Soc.*, 68(2): 206 – 213.
- Mir SH, Mir GM, 2016. Lekking behaviour and male-male rivalry in the melon fly *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae). *J. Insect Behav.*, 29(4): 379 – 384.
- Miranda X, 2000. Sexual dimorphism in the arista of *Ceratitis capitata* (Diptera, Tephritidae) and its possible importance in courtship. *J. N. Y. Entomol. Soc.*, 108(3): 339 – 348.
- Ngumbi EN, Jordan M, Fadamiro HY, 2012. Comparison of associative learning of host-related plant volatiles in two parasitoids with different degrees of host specificity, *Cotesia marginiventris* and *Microplitis croceipes*. *Chemoecology*, 22(4): 207 – 215.
- Nishida R, Tan KH, Fukami H, 1988b. *Cis*-3,4-dimethoxycinnamyl alcohol from the rectal glands of male oriental fruit fly, *Dacus dorsalis*. *Chem. Express*, 3: 207 – 210.
- Nishida R, Tan KH, Serit M, Lajis NH, Sukari AM, Takahashi S, Fukami H, 1988a. Accumulation of phenylpropanoids in the rectal glands of males of the oriental fruit fly, *Dacus dorsalis*. *Experientia*,

- 44(6): 534–536.
- Nufio CR, Papaj DR, 2001. Host marking behavior in phytophagous insects and parasitoids. *Entomol. Exp. Appl.*, 99(3): 273–293.
- Ohinata K, Jacobson M, Kobayashi RM, Chambers DL, Fujimoto MS, Higa HH, 1982. Oriental fruit fly and melon fly: biological and chemical studies of smoke produced by males. *J. Environ. Sci. Health*, 17(2): 197–216.
- Opp SB, Spisak SA, Telang A, Hammond SS, 1996. Comparative mating systems of two *Rhagoletis* species: the adaptive significance of mate guarding. In: McPherson BA, Steck GJ eds. *Fruit Fly Pests: A World Assessment of Their Biology and Management*. CRC Press, Boca Raton. 43–49.
- Papaj DR, Averill AL, Prokopy RJ, Wong TTY, 1992. Host-marking pheromone and use of previously established oviposition sites by the Mediterranean fruit fly (Diptera: Tephritidae). *J. Insect Behav.*, 5(5): 583–598.
- Papaj DR, Roitberg BD, Opp SB, 1989. Serial effects of host infestation on egg allocation in the Mediterranean fruit fly: a rule of thumb and its functional significance. *J. Anim. Entomol.*, 58(3): 955–970.
- Papaj DR, Roitberg BD, Opp SB, Aluja M, Prokopy RJ, Wong TTY, 1990. Effect of marking pheromone on clutch size in the Mediterranean fruit fly. *Physiol. Entomol.*, 15(4): 463–468.
- Parri S, Alatalo RV, Kotiaho JS, Mappes J, Rivero A, 2002. Sexual selection in the wolf spider *Hygrolycosa rubrofasciata*: female preference for drum duration and pulse rate. *Behav. Ecol.*, 13(5): 615–621.
- Pereira R, Yuval B, Liedo P, Teal PEA, Shelly TE, McInnis DO, Hendrichs J, 2012. Improving sterile male performance in support of programmes integrating the sterile insect technique against fruit flies. *J. Appl. Entomol.*, 137(Suppl. 1): 178–190.
- Pérez-Staples D, Shelly TE, Yuval B, 2012. Female mating failure and the failure of “mating” in sterile insect programs. *Entomol. Exp. Appl.*, 146(1): 66–78.
- Perkins MV, Fletcher MT, Kitching W, Drew RAI, Moore CJ, 1990b. Chemical studies of rectal gland secretions of some species of *Bactrocera dorsalis* complex of fruit flies (Diptera: Tephritidae). *J. Chem. Ecol.*, 16(8): 2475–2487.
- Perkins MV, Kitching W, Drew RAI, Moore CJ, König WA, 1990a. Chemistry of fruit flies: composition of the male rectal gland secretions of some species of South-East Asian Dacinae. Re-examination of *Dacus cucurbitae* (melon fly). *J. Chem. Soc., Perkin Trans. 1*, 4: 1111–1117.
- Piñero JC, Mau RFL, Vargas RI, 2011. A comparative assessment of the response of three fruit fly species (Diptera: Tephritidae) to a spinosad-based bait; effect of ammonium acetate, female age, and protein hunger. *Bull. Entomol. Res.*, 101(4): 373–381.
- Piñero JC, Souder SK, Vargas RI, 2013. Residual attractiveness of a spinosad-containing protein-based bait aged under variable condition to *Bactrocera dorsalis* and *B. cucurbitae* (Diptera: Tephritidae) wild females in Hawaii. *Fla. Entomol.*, 96(3): 1077–1083.
- Poramarcom R, Boake CRB, 1991. Behavioural influences on male mating success in the Oriental fruit fly, *Dacus dorsalis* Hendel. *Anim. Behav.*, 42(3): 453–460.
- Pritchard G, 1969. The ecology of a natural population of Queensland fruit fly, *Dacus tryoni*. II. The distribution of eggs and its relation to behaviour. *Austr. J. Zool.*, 17(2): 293–311.
- Prokopy RJ, Green TA, Olson WA, Vargas RF, Kaneshia D, Wong TY, 1989. Discrimination by *Dacus dorsalis* females (Diptera: Tephritidae) against larval infested fruit. *Fla. Entomol.*, 72(2): 319–323.
- Prokopy RJ, Koyama J, 1982. Oviposition site partitioning in *Dacus cucurbitae*. *Entomol. Exp. Appl.*, 31(4): 428–432.
- Quilici S, Frank A, Peppuy A, Dos Reis Correia E, Mouniama C, Blard F, 2002. Comparative studies of courtship behavior of *Ceratitis* spp. (Diptera: Tephritidae) in Reunion Island. *Fla. Entomol.*, 85(1): 138–142.
- Raghu S, Drew RAI, Clarke AR, 2004. Influence of host plant structure and microclimate on the abundance and behaviour of a tephritid fly. *J. Insect Behav.*, 17(2): 179–190.
- Renou M, Guerrero A, 2000. Insect parapheromones in olfaction research and semiochemical-based pest control strategies. *Annu. Rev. Entomol.*, 45: 605–630.
- Roan CC, Flitters NE, Davis CJ, 1954. Light intensity and temperature as factors limiting the mating of the oriental fruit fly. *Annu. Entomol. Soc. Am.*, 47(4): 593–594.
- Roitberg BD, Cairl RS, Prokopy RJ, 1984. Oviposition deterring pheromone influences dispersal distance in tephritid fruit flies. *Entomol. Exp. Appl.*, 35(3): 217–220.
- Roitberg BD, van Lenteren JC, van Alaphen JJM, Galis F, Prokopy RJ, 1982. Foraging behaviour of *Rhagoletis pomonella*, a parasite of hawthorn (*Crataegus viridis*), in nature. *J. Anim. Ecol.*, 51(1): 307–325.
- Schiestl RHWS, Chan RD, Gietz RDM, Hastings PJ, 1989. Safrole, eugenol and methyleugenol induce intrachromosomal recombination in yeast. *Mutat. Res.*, 224(4): 427–436.
- Segura D, Petit-Marty N, Sciuirano R, Vera T, Calcagno G, Allinghi A, Cendra PG, Cladera J, Vilardi J, 2007. Lekking behavior of *Anastrepha fraterculus* (Diptera: Tephritidae). *Fla. Entomol.*, 90(1): 154–162.
- Seikizawa J, Shibamoto T, 1982. Genotoxicity of safrole-related chemical in microbial test systems. *Mutat. Res.*, 101(2): 127–140.
- Shelly T, Edu J, Pahio E, 2012. Mate choice by lekking males: evidence from the Mediterranean fruit fly from field cage trials (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.*, 105(2): 368–376.
- Shelly T, Epsky N, Jang EB, Reyes-Flores J, Vargas RI, 2014. Trapping and the Detection, Control, and Regulation of Tephritid Fruit Flies. Springer, Netherlands.
- Shelly TE, 1999. Defense of oviposition sites by female oriental fruit flies (Diptera: Tephritidae). *Fla. Entomol.*, 82(2): 339–346.
- Shelly TE, 2000. Flower-feeding affects mating performance in male oriental fruit flies *Bactrocera dorsalis*. *Ecol. Entomol.*, 25(1): 109–114.
- Shelly TE, 2001. Feeding on methyl eugenol and *Fagraea berteriana*

- flowers increases long-range female attraction by males of the oriental fruit fly (Diptera: Tephritidae). *Fla. Entomol.*, 84(4): 634 – 640.
- Shelly TE, 2010. Effects of methyl eugenol and raspberry ketone/cue lure on the sexual behavior of *Bactrocera* species (Diptera: Tephritidae). *Appl. Entomol. Zool.*, 45(3): 349 – 361.
- Shelly TE, Kaneshiro KY, 1991. Lek behavior of the Oriental fruit fly, *Dacus dorsalis*, in Hawaii (Diptera: Tephritidae). *J. Insect Behav.*, 4(2): 235 – 241.
- Sivinski J, Aluja M, Dodson G, Freidberg A, Headrick D, Kaneshiro K, Landolt P, 2000. Topics in the evolution of sexual behavior in the Tephritidae. In: Aluja M, Norrbom AL eds. *Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior*. CRC Press, Boca Raton. 751 – 792.
- Smith DC, Prokopy RJ, 1980. Mating behavior of *Rhagoletis pomonella* (Diptera: Tephritidae). VI. Site of early-season encounters. *Can. Entomol.*, 112(6): 585 – 590.
- Smith DC, Prokopy RJ, 1982. Mating behaviour of *Rhagoletis mendax* (Diptera: Tephritidae) flies in nature. *Ann. Entomol. Soc. Am.*, 75(4): 388 – 392.
- Tan KH, Nishida R, Jang EB, Shelly TE, 2014. Pheromones, male lures, and trapping of tephritid fruit flies. In: Shelly T, Epsky N, Jang EB, Reyes-Flores J, Vargas RI eds. *Trapping and the Detection, Control, and Regulation of Tephritid Fruit Flies*. Springer, Netherlands. 15 – 74.
- Taylor PW, Yuval B, 1999. Postcopulatory sexual selection in Mediterranean fruit flies: advantages for large and protein-fed males. *Anim. Behav.*, 58(2): 247 – 254.
- Tokushima I, Orankanok W, Tan KH, Ono H, Nishida R, 2010. Accumulation of phenylpropanoid and sesquiterpenoid volatiles in male rectal pheromonal glands of the guava fruit fly, *Bactrocera correcta*. *J. Chem. Ecol.*, 36(12): 1327 – 1334.
- Tychsen PH, 1978. Mating behaviour of the Queensland fruit fly, *Dacus tryoni* (Diptera: Tephritidae), in field cages. *Aust. J. Entomol.*, 16(4): 459 – 465.
- University of Hawaii, 2015. Dacine Fruit Flies of the Asia-Pacific. University of Hawaii at Manoa. <http://www.herbarium.hawaii.edu/fruitfly/index.php>. [accessed on 10 January 2015]
- Vargas RI, Piñero JC, Leblanc L, 2015. An overview of pest species of *Bactrocera* fruit flies (Diptera: Tephritidae) and the integration of biopesticides with other biological approaches for their management with a focus on the Pacific Region. *Insects*, 6(2): 297 – 318.
- Vargas RI, Shelly TE, Leblanc L, Piñero JC, 2010. Recent advances in methyl eugenol and cue lure technologies for fruit fly detection, monitoring and control in Hawaii. In: Liwack G ed. *Vitamins and Hormones*, Vol 83. Elsevier Inc., Academic Press, Burlington. 575 – 596.
- Wan FH, Guo JY, Zhang F, 2009. *Research on biological invasions in China*. Science Press, Beijing.
- Wang JT, Dong YC, Li ZK, Li SB, Niu CY, 2013. Overview of the use of the sterile insect technique to control the Chinese citrus fruit fly. *Chin. J. App. Entomol.*, 50(3): 848 – 852. [王金涛, 董永成, 李宗楷, 黎少波, 牛长纓, 2013. 昆虫不育技术防治柑橘大实蝇研究概况. *应用昆虫学报*, 50(3): 848 – 852]
- Wee SL, Munir MA, Hee AKW, 2017. Attraction and consumption of methyl eugenol by male *Bactrocera umbrosa* Fabricius (Diptera: Tephritidae) promotes conspecific sexual communication and mating performance. *Bull. Entomol. Res.*, 19: 1 – 9.
- Whittier TS, Kaneshiro KY, 1995. Intersexual selection in the Mediterranean fruit fly: does female choice enhance fitness? *Evolution*, 49(5): 990 – 996.
- Whittier TS, Kaneshiro KY, Prescott LD, 1992. Mating behavior of Mediterranean fruit flies (Diptera: Tephritidae) in a natural environment. *Ann. Entomol. Soc. Am.*, 85(2): 214 – 218.
- Widemo F, Owens IPF, 1999. Size and stability of vertebrate leks. *Anim. Behav.*, 58(6): 1217 – 1221.
- Wilkinson GS, Johns PM, 2005. Sexual selection and the evolution of mating systems in flies. In: Yeates DK, Weigmann BM eds. *The Biology of the Diptera*. Columbia University Press, New York. 312 – 339.
- Wu KM, 2013. *Studies on the Sex Pheromone of Chinese Citrus Fly, Bactrocera minax*. MSc Thesis, Southwest University, Chongqing. [武可明, 2013. 柑橘大实蝇性信息素的初步研究. 重庆: 西南大学硕士学位论文]
- Yuval B, Ben-Ami E, Behar A, Ben-Yosef M, Jurkevitch E, 2013. The Mediterranean fruit fly and its bacteria – potential for improving sterile insect technique operations. *J. Appl. Entomol.*, 137(s1): 39 – 42.
- Zhang H, Fletcher MT, Avery JW, Kitching W, 1997. A suite of odd and even carbon-numbered spiroacetals in *Bactrocera latifrons*. Synthesis and stereochemistry. *Tetrahedron Lett.*, 38(19): 3477 – 3478.
- Zhou GD, Moorthy B, Bi J, Donnelly KC, Randerath K, 2007. DNA adducts from alkoxyallylbenzene herb and spice constituents in cultured human (HepG2) cells. *Environ. Mol. Mutagen.*, 48(9): 715 – 721.
- Zhou Q, Liu L, 2013. Research on active components of sex pheromone and attractants in citrus fruit fly *Bactrocera minax*. In: *Proceedings of 9th Conference of the Chinese Association of Chemical Ecology*, Shenyang. Ecological Society of China. 52. [周琼, 刘路, 2013. 柑橘大实蝇性信息素活性成分及其性诱剂的研制. 见: 第九届全国化学生态学学术研讨会论文集, 沈阳. 中国生态学会. 52]

(责任编辑: 赵利辉)