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垂叶榕上16种榕小蜂的种群动态

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摘要: 传粉榕小蜂和榕树的互利共生是传粉昆虫与植物间协同进化的典范。在榕果(榕树的隐头状花序)内, 还生活着多种非传粉榕小蜂。这些生活在密闭榕果内由传粉榕小蜂和非传粉榕小蜂组成的群落对研究群落生态学有很大价值。然而, 对生存在单一榕树的榕果内的所有榕小蜂的种群动态了解很少, 特别是缺少相对长期的连续数据。通过野外近3a观察和采样, 研究了垂叶榕榕小蜂群落结构和榕小蜂的种群动态。共记录榕小蜂16种; 各种榕小蜂根据发生规律可分为常见种和偶见种, *Eupristina koningsbergeri*, *Philotrypesis* sp. 1, *Philotrypesis* sp. 4, *Philotrypesis* sp. 5, *Sycoscapter* sp. 1, *Walkerella benjamini*, *Walkerella* sp. 1, *Sycophila* sp. 2, *Sycobia* sp. 2为常见种; *Sycobia* sp. 1, *Acophila* sp. 1, *Sycophila* sp. 1, *Ormyrus* sp. 1等为偶见种。每种榕小蜂在单果上的数量随季节呈波动变化, 季节对榕小蜂群落的多样性和均匀性无显著影响。除了传粉榕小蜂外, *Sycoscapter* sp. 1也是优势种类之一。传粉榕小蜂的数量与非传粉榕小蜂总数间呈显著负相关。传粉榕小蜂与非传粉榕小蜂几乎都呈负相关, 而与*Walkerella* sp. 1在数量上呈显著正相关。*Sycobia* sp. 2与*Sycophila* sp. 2在同一瘿中出现, 数量上呈显著正相关。但其它非传粉榕小蜂种类在数量上的相关性较为复杂, 可能是造成各种榕小蜂数量波动的一个原因。

关键词: 榕树; 榕小蜂; 群落结构; 种群动态

Population dynamics of 16 fig wasp species in *Ficus benjamina*

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Abstract The mutualism between figs and pollinating fig wasps is a classic example for studying the origin, equilibrium mechanisms and evolution of mutualism, resource conflicts, and sex allocation. Figs (*Ficus* spp.) depend on wasps for transmission of their pollen, and fig wasps depend on fig inflorescences (syconia) for the completion of their life cycles. Non-pollinating fig wasps also live in figs, with different influences on the mutualism due to different biological habits. These communities, which consist of pollinating and non-pollinating fig wasps in the closed syconia, could be valuable for studies of community ecology. However, we have little knowledge about the population dynamics of the entire community of species associated with single fig species, especially over the long term. We have investigated community structure of fig wasps exploiting syconia of *Ficus benjamina*, a monoecious, commonly cultivated tree, for about 3 years in Chinese Academy of Tropical Agricultural Sciences, Danzhou, Hainan Province. We collected and dissected the mature figs from the surrounding trees, sought out all wasps even if some of them were still living in galls, identified the species and counted individuals. We found 16 species of fig wasps, including one obligate pollinator, *Eupristina koningsbergeri*, and 15 non-pollinating fig wasps belonging to 8 genera of Chalcidoidea, including 1 newly recorded species of *Sycoscapter* and 2 new records of *Sycophila*. Common species included *Eupristina koningsbergeri* and such non-pollinating fig wasps as *Philotrypesis*

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sp. 1, *Philotrypesis* sp. 4, *Philotrypesis* sp. 5, *Sycoscapter* sp. 1, *Walkerella benjamini*, *Walkerella* sp. 1, *Sycophila* sp. 2 and *Sycobia* sp. 2. The pollinator was dominant and nearly as frequent as the non-pollinators, with a large range of variation in number among months. Besides the pollinator, *Sycoscapter* sp. 1 made up the largest proportion of non-pollinators, while *Philotrypesis* sp. 5 was the rarest. The other 7 species were only occasionally caught, including *Sycoscapter* sp. 2, *Sycobia* sp. 1, *Acophila* sp. 1, *Sycophila* sp. 1, *Sycophila* sp. 3, *Sycophila* sp. 4, *Ormyrus* sp. 1. These species were not present every month, and fewer than 10 wasps of each were recorded per fig. The presence of these species usually did not distort the number of other common species. But when resources were limited, with small populations of the community, the occasional species had influence on the common non-pollinators. All the fig wasps varied in population density per syconium across months. A maximum of 589 fig wasps were found in a single fig, and 155.38 on average in wet season. While in dry season the numbers were 335 and 99.84 per fig. But there were no significant changes in the community structure between dry or wet seasons. The number of pollinators was negatively correlated with those of each of the non-pollinating fig wasps, except for *Walkerella* sp. 1, which was positively correlated with the pollinator. Sometimes, *Sycobia* sp. 2 and *Sycophila* sp. 2 both occurred in the same gall, and were positively correlated in number. However, the numerical relationships among the other non-pollinating fig wasps were very complicated. We will examine relationships among these non-pollinating fig wasps in the future.

Key Words: *Ficus*; fig wasp; community structure; population dynamics

榕树是荨麻目桑科榕属 (*Ficus*)植物的总称,广泛分布于热带和亚热带地区,目前已知约 750种[1]。除少数种之外[2],每一种榕树都依赖专一的传粉榕小蜂传粉才能进行有性繁殖,而传粉榕小蜂也只能依靠榕果内的雌花子房资源来繁衍后代,完成其生活史[3-7]。榕树和传粉榕小蜂所组成的专一的互惠共生体系是研究动植物间协同进化的典型材料[8-9]。

作为热带雨林生态系统中的一类关键植物,榕树为许多动物提供食物及栖息场所[10-13],这其中也包括在榕果内生活的各种非传粉榕小蜂(non-pollinator fig wasp, NPFW)。非传粉小蜂的种类数量因榕树而异,如西双版纳高榕(*Ficus altissima*)的榕果内共生活着 25种非传粉小蜂[14],有的榕树甚至供养着多达 29种非传粉榕小蜂[15]。非传粉榕小蜂与传粉榕小蜂同时在榕果内生活,但却可以与互惠共生体系稳定共存,所以非传粉小蜂对榕-蜂共生体系的作用也越来越受到关注[16-17],已有研究证明非传粉榕小蜂会对互惠共生体系产生负面影响[18-19]。

非传粉榕小蜂中的寄生者一般利用传粉榕小蜂,但也可能利用其它非传粉榕小蜂种类[4]。对 *F. hispidioides*的研究表明,非传粉榕小蜂 *Apocrypta* 依赖于另外一种非传粉榕小蜂 *Apocryptophagus*生活[20-22]。在对叶榕上,*Apocrypta bakeri* 可以利用 *Philotrypesis pilosa*, *Philotrypesis* sp. 以及传粉榕小蜂 *Ceratosolen solmsi marchali*[23]。垂叶榕(*Ficus benjamina*)的榕果中除了传粉榕小蜂 *Eupristina koningsbergeri*外,存在至少 12种非传粉榕小蜂[24]。但由于榕果是一个密闭、黑暗的环境,体积小,果内榕小蜂种类繁多,种群密度非常大,食性复杂,无法直接观测确定各种榕小蜂数量变化及各种类之间的关系。本研究通过 3a的采样,对垂叶榕榕果内的各种榕小蜂种群数量的季节性变化进行了研究,记录了不同时期榕果内榕小蜂群落组成,并试从数量角度对传粉榕小蜂与非传粉榕小蜂的关系,以及非传粉榕小蜂之间关系进行探讨。

1 材料与方法

1.1 研究地点

野外调查主要在海南省儋州市华南热带农业大学和中国热带农业科学院校园内及周边地区完成。儋州市位于海南岛西北部,濒临北部湾,距省会海口市 130km,为典型的热带海洋性季风气候,明显地分为两个季节:每年 5—10月份为雨季,11月一翌年 4月份为旱季。年平均气温 23—25℃,2月份最低 17—22℃,极端低温在 5℃左右,7月份最高 26—29℃。年均降水量 1500—1800mm,其中 70%—90%集中在雨季,雨季降雨非

常规律,主要集中在每天下午,年平均相对湿度 83%。

1.2 研究材料

垂叶榕(*F. benjamina*)隶属于榕亚属(*Urostigma*),雌雄同株。主要分布于我国的广东、广西、贵州、台湾、海南、云南等省,在国外分布于不丹、柬埔寨、印度、老挝、马来西亚、尼泊尔、新几内亚、菲律宾、泰国、越南、澳大利亚北部、太平洋岛屿等地。垂叶榕榕果一般成对生于叶腋,榕果发育属于典型的株内同步,株间异步,树每年开花次数不规律。榕果呈球形或扁球形,成熟时黄色至红色,直径 0.8—1.5cm。垂叶榕作为一种观赏树木,常用于庭院和行道绿化。

1.3 研究方法

2006年 2月—2008年 7月,每月上旬选取榕果当月成熟的垂叶榕 1—2株,在榕果颜色变黄,果壁开始变软,果内小蜂即将羽化出蜂前,随机采集榕果 30—40个带回实验室。室内用直径 2cm,长 5cm的透明塑料管进行单果分装,为保证透气,在盖子上打孔,盖内垫 120目的绢纱,防止羽化小蜂逃出。将榕果掰开辅助小蜂羽化出果,待瘿花内所有小蜂羽化完成时,收集每个果内羽化出来的小蜂,置于 95%的酒精内保存,并做好采集记录和标签。对于未完全出瘿的榕小蜂,在 Nikon SMZ645体视显微镜下,用镊子直接取出。对收集到的榕小蜂进行分类鉴定,统计单果内各种小蜂的数量。

榕果中各类小蜂数量间以及传粉榕小蜂和非传粉榕小蜂总量间分别进行相关分析,分析在 SPSS11.5中完成。采用物种丰富度、Shannon-Wiener多样性指数、Pielou均匀度指数以及重要值分析垂叶榕榕果内小蜂的群落结构[25-26]。

Shannon-Wiener多样性指数:

$$H = -\sum Pi\ln Pi \tag{1}$$

Pielou均匀度指数:

$$J = H / \ln S \tag{2}$$

重要值:

$$IV = 相对密度 + 相对频度 \tag{3}$$

式中, S为小蜂的总种数, Pi为种 i的个体数占总个体数的比例。相对密度为单个批次中某种小蜂总数占全部小蜂总数的比例, 相对频度为单个批次中某种小蜂出现的样果数占总样果数的比例。

2 结果与分析

2.1 垂叶榕榕小蜂群落结构

调查共获得榕小蜂隶属于膜翅目小蜂总科 8个属 16个种(表 1),单批次出蜂种类最多为 14种,单果出蜂种类最多 12种。群落中各种小蜂分为常见种和偶见种两类,常见种发生有连续性,包括 *Eupristina koningsbergeri*, *Philotrypesis* sp.1, *Philotrypesis* sp.4, *Philotrypesis* sp.5, *Sycoscapter* sp.1, *Walkerella benjamini*, *Walkerella* sp.1, *Sycophila* sp.2, *Sycobia* sp.2共 9种,其中 *Sycophila* sp.2, *Sycobia* sp.2体型大,其他种类体型小。除 9个常见种外,其他种类全为偶见种,包括 *Sycoscapter* sp.2, *Sycobia* sp.1, *Acophila* sp.1, *Sycophila* sp.1, *Sycophila* sp.3, *Sycophila* sp.4, *Ormyrus* sp.1。这些种类榕小蜂发生数量极少,发生没有

表 1 垂叶榕榕果内榕小蜂种类调查表

Table 1 Specie of the fig wasps in *Ficus benjamina*

科 Family	亚科 Subfamily	种名 Species
Agaonidae	Agaoninae	*Eupristina koningsbergeri*
Pteromalidae	Epichrysomallinae	*Sycobia* sp.1; *Sycobia* sp.2; *Acophila* sp.1
	Sycoryctinae	*Philotrypesis* sp.1; *Philotrypesis* sp.4; *Philotrypesis* sp.5; *Sycoscapter* sp.1; *Sycoscapter* sp.2
	Otitesellinae	*Walkerella benjamini*; *Walkerella* sp.1
Eurytomidae	Eurytominae	*Sycophila* sp.1; *Sycophila* sp.2; *Sycophila* sp.3; *Sycophila* sp.4
Ormyridae		*Ormyrus* sp.1

连续性,甚至连续几个月采集不到,除 *Sycoscapter* sp. 2体型较小之外,其他种类都相对大型。偶见种每批次总数量一般不超过10头,单果出蜂量一般不超过3头。但 *Acophila* sp. 1例外,在4月份会有大爆发,每果能出蜂7—9头,最多达14头。

全年各种榕小蜂存在显著的月度数量变化,旱季单果出蜂量变化幅度很大,平均单果出蜂量为155.38头/果,最大可达589头/果;雨季变化幅度相对较小,平均单果出蜂量为99.84头/果,最大可达335头/果。分析旱季和雨季小蜂群落的多样性指数和均匀度指数看出,旱季和雨季垂叶榕榕小蜂群落结构的多样性指数间无显著差异($P > 0.05$),均匀度指数也无显著差异($P > 0.05$)(表2)。

表2 不同季节垂叶榕隐头果内小蜂群落的多样性、均匀度指标

Table 2 Species diversity index of fig wasp community inside the syconium of *F. benjamina* in different seasons

	旱季 Dry Season									
	06-02	06-04	07-03	07-11	07-11	07-12	08-01	08-03	08-04	08-04
H	1.56	1.78	1.88	1.76	1.43	0.47	0.76	1.63	0.28	0.14
J	0.22	0.24	0.24	0.21	0.16	0.06	0.09	0.24	0.06	0.02
	雨季 Wet Season									
	06-05	06-06	06-06	06-09	07-05	07-08	07-09	07-10	08-07	
H	1.69	1.45	1.80	1.47	1.28	1.06	0.22	1.49	1.57	
J	0.23	0.22	0.25	0.18	0.21	0.13	0.03	0.18	0.20	

从发生数量来看,传粉榕小蜂在群落中始终处于优势地位,数量与非传粉榕小蜂总量基本相当,旱季占52.39%,$IV_{\text{旱季}} = 1.24$;雨季占42.69%,$IV_{\text{雨季}} = 1.19$。各种非传粉榕小蜂中 *Sycoscapter* sp. 1数量最大,旱季占16.62%,$IV_{\text{旱季}} = 0.74$;雨季占23.08%,$IV_{\text{雨季}} = 0.9$。

2.2 榕小蜂间关系

垂叶榕榕小蜂种类间数量相关分析见表3。传粉榕小蜂数量与非传粉榕小蜂总数间呈显著负相关。除 *Walkerella* sp. 1外,传粉榕小蜂与非传粉榕小蜂都呈负相关,而只有 *Philotrypesis* sp. 1和 *Walkerella benjamini* 相关性有统计学意义,说明非传粉榕小蜂对传粉榕小蜂有负面影响,但作用大小因种类而异。传粉榕小蜂与 *Walkerella* sp. 1在数量上呈显著正相关。*Sycobia* sp. 2与 *Sycophila* sp. 2在同一虫瘿中出现,数量上呈显著正相关。但其它类型非传粉榕小蜂间数量上的相关性较为复杂(表3)。

表3 垂叶榕榕小蜂种群数量相关性

Table 3 The correlation of population number of fig wasps in *F. benjamina*

	NPFW	*P.* sp. 1	*P.* sp. 4	*P.* sp. 5	*Sycoscapter* sp. 1	*W. benjamini*	*Sycobia* sp. 2	*Sycophila* sp. 2	*W.* sp. 1
P. sp. 1	0.141**								
P. sp. 4	0.424**	−0.152**							
P. sp. 5	0.263**	0.164**	0.184**						
Sycoscapter sp. 1	0.793**	−0.174**	0.362**	0.123*					
W. benjamini	0.359**	0.494**	−0.061	0.13*	−0.031				
Sycobia sp. 2	0.339**	−0.037	−0.005	0.06	−0.054	0.093			
Sycophila sp. 2	0.330**	−0.005	−0.16*	−0.051	0.007	0.079	0.580**		
W. sp. 1	0.477**	−0.083	0.082	0.122**	0.399**	−0.054	−0.16*	−0.001	
E. koningsbergeri	−0.118*	−0.257**	−0.007	−0.034	−0.032	−0.285**	−0.096	−0.168**	0.318**

** $P < 0.01$, * $P < 0.05$

3 讨论

干季和湿季榕小蜂的群落结构没有显著差异,而全年各种榕小蜂单果发生数量有月度波动变化(图1)。传粉榕小蜂为独立造瘿,而非传粉榕小蜂中,存在独立造瘿、寄居和寄生者等多种类型[27]。非传粉榕小蜂中

的寄生者可以利用传粉榕小蜂，但一些种类也可能利用其它非传粉榕小蜂种类[4]，如 *Apocrypta* 依赖于另外一种非传粉榕小蜂 *Apocryptophagus* 生活[20-22]，一些非传粉榕小蜂可以寄生（或寄居）多种榕小蜂，如 *A. bakeri* 可能会利用 *Philotrypesis pilosa*, *Philotrypesis* sp 以及传粉榕小蜂 *Ceratosolen solmsimarchali*[23]。在垂叶榕榕小蜂种类中，除传粉榕小蜂之外，*Walkerella benjamini*, *Walkerella* sp 1, *Acophila* sp 1, *Sycobia* sp 2为造瘿者[24]。而其它种类与这些造瘿类小蜂间关系较为复杂。非传粉榕小蜂之间复杂的依赖关系是导致各个种类发生数量波动的重要原因。除此之外，由于榕树一般具有株内同步、株间异步的开花物候学特点[4]，榕小蜂的可获得性也可能是影响榕小蜂种群密度波动的重要原因。

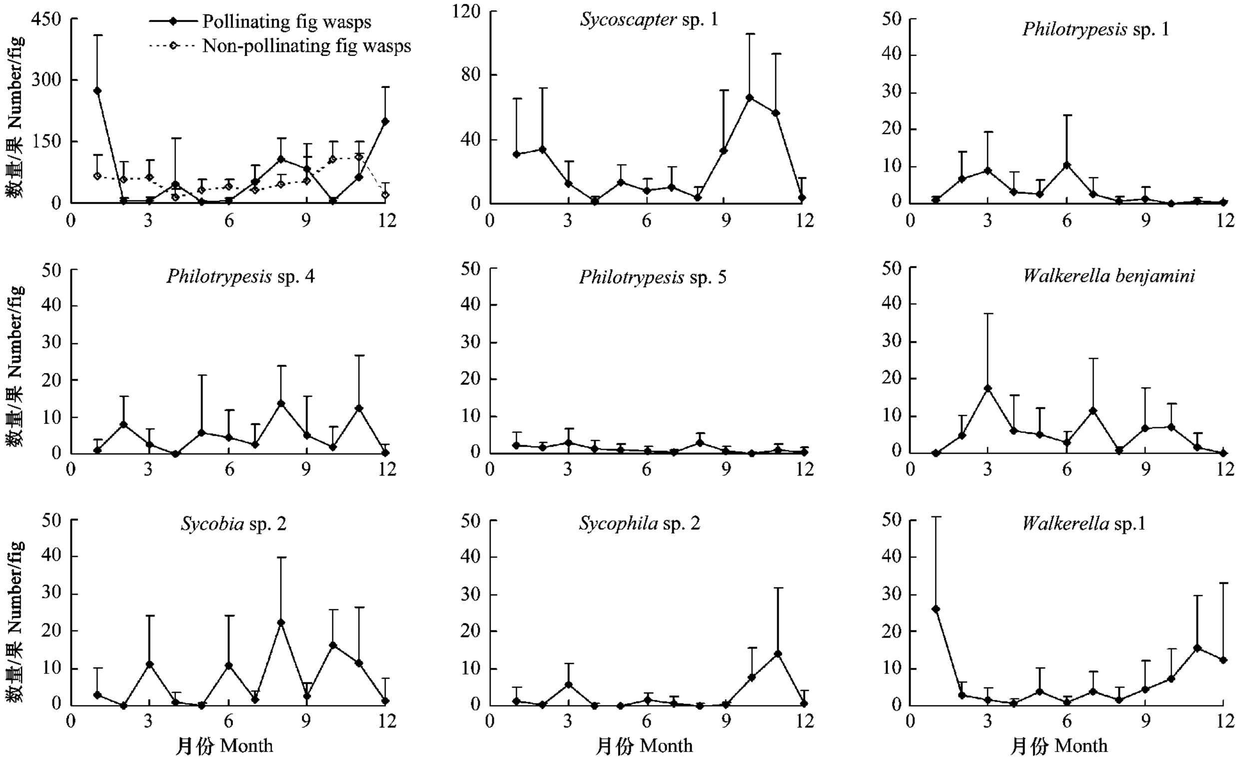

图 1 垂叶榕榕小蜂种群动态

Fig 1 Population dynamic of fig wasps in *F. benjamina*

榕小蜂必须依赖榕果才能完成其整个生活史[28]。除传粉榕小蜂外，非传粉榕小蜂也对特定的榕树存在一定的寄主专一性[29]。获得到 7种偶见种，为什么偶见种与常见种数量差异如此之大？偶见种在不发生的月份里也许是出于以下原因：(1)受环境影响而产生滞育，导致存活率较低；(2)发生寄主转移在其它种类榕树上甚至是榕树以外的寄主上生活[30-31]；(3)榕树外有很多的蚂蚁，蚂蚁能强烈地影响非传粉小蜂在榕果上产卵，而对传粉榕小蜂的产卵影响不大，这种影响间接有利于榕树和传粉榕小蜂的繁殖[32]，也可能是造成出现偶见种的原因。

从数量上分析，传粉榕小蜂是优势种，出蜂量最大，与非传粉榕小蜂总量大致相当，各占一半。但几乎所有非传粉榕小蜂都与传粉榕小蜂呈负相关，非传粉榕小蜂总量与传粉榕小蜂数量呈显著负相关，说明非传粉榕小蜂对传粉榕小蜂有明显的负面作用[4, 33-35]。而 *Walkerella* sp 1与传粉榕小蜂数量上呈正相关关系，野外观察表明，*Walkerella* sp 1为独立造瘿者，在榕果接受期（传粉榕小蜂入果期）前产卵；传粉榕小蜂的成功造瘿可能促进了 *Walkerella* sp 1的成活率增加，从而产生 *Walkerella* sp 1对传粉榕小蜂在数量上的依赖性。

Sycophila 与 *Sycobia* 两个属在很多种榕树上都是同时出现[36]，在观察记录中，同一虫瘿内同时出现过 *Sycobia* sp 2雌虫与 *Sycophila* sp 2雄虫的情况。在数量上，两者间呈显著正相关，表明 *Sycophila* sp 2可能依赖于造瘿的 *Sycobia* sp 2而存在，但由于 *Sycophila* 属既有寄生性的又有寄居性的种类[37-38]，因此不能准确

判定 *Sycophila* sp. 2与 *Sycobia* sp. 2的关系。垂叶榕榕果中的其它类型非传粉榕小蜂数量上的相关性比较复杂,还需根据食性进一步确定它们之间关系。

对于雌雄同株榕树而言,在榕果内存在传粉榕小蜂和种子之间的资源冲突;传粉榕小蜂在理论上可以利用榕果内的几乎全部的子房资源,但实际上无论传粉榕小蜂数量多大,榕果内仍然有种子存在[4, 39-41]。榕小蜂群落没有占据所有的小花资源,榕果内是不饱和的[33, 42]。

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