

窄切叶蜂筑巢生物学特性研究*

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摘要 【目的】研究窄切叶蜂 *Megachile rixator* 的筑巢生物学特性, 为开展该物种的保护、人工管理和驯化提供数据支撑。【方法】2015年8月至2020年7月, 在江西省德兴市新岗山镇的 BEF-China 实验样地设置了 88 个采样点, 使用了标准化的人工巢管诱集窄切叶蜂筑巢, 并观察其生物学特性。【结果】试验期间共采集到窄切叶蜂筑巢巢管 199 根, 巢室 866 个, 其中羽化 347 头成虫, 未羽化死亡率占 60%; 后代雌性/雄性数量比例为 0.57; 雌性每年 5-11 月使用植物叶片建造巢室, 进行筑巢活动; 一头雌蜂平均每次建造巢室 (3.75 ± 2.24) 个; 巢口平均直径 (10.00 ± 2.37) mm, 偏向于在巢管内径为 11-13 mm 的范围内筑巢; 当年 9 月以后所产后代滞育, 以预蛹期越冬; 后代性比(雌性数量/雄性数量)在 5 月最高, 之后逐月递减, 但在 11 月又有所增加; 在巢管内径 5-7 mm 的范转内后代性比最低, 且随巢口内径增加而升高, 但在内径 13-15 mm 范围内又下降。【结论】窄切叶蜂是典型的独栖性切叶蜂, 每年从春末到秋末持续发生筑巢活动, 使用植物叶片建造巢室, 呈多化性; 每次筑巢会产下多个后代, 死亡率较高; 后代性比偏向雄性; 可在当年 9-11 月使用较粗内径的巢管收集雌性窄切叶蜂。本研究结果为窄切叶蜂授粉的应用提供参考。

关键词 切叶蜂; 独栖性蜜蜂; 亚热带森林; 人工巢管; 性比

Nesting characteristics of *Megachile rixator* (Hymenoptera: Megachilidae)

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Abstract 【Objectives】To investigate the nesting biology of *Megachile rixator* in order to provide a theoretical basis for the protection, artificial management and domestication of this pollinating bee species. 【Methods】A total of 88 sample plots were established at the BEF-China experimental site in Xingangshan town, Dexing city, Jiangxi province, China between August 2015 and July 2020. Standardized trap-nests were used to collect *M. rixator* whose biological characteristics were then recorded and analyzed. 【Results】A total of 866 nests were recorded, 347 of which were successful with an overall mortality

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rate of 60%. The ratio of female to male offspring was 0.57. Females built nests using plant leaves from May to November, building an average of (3.75 ± 2.24) nests each time. The average diameter of nests was (10.00 ± 2.37) mm, and nests tended to be within the range of 11-13 mm. Diapause occurred after September and individuals overwintered in the pre-pupal stage. The sex ratio of offspring peaked in May after which it decreased each month until increasing again in November. The sex ratio of offspring was lowest in nests with a diameter of 5-7 mm, was higher in nests of moderate diameter, and lower in nests with a diameter of 13-15 mm. **[Conclusion]** *M. rixator* is a typical solitary, leafcutter bee species that uses plant leaves to build nests. It is, however, polymorphic. Each nest produces multiple offspring and has a high mortality rate. Nesting takes place continuously from late spring to late fall each year. The sex ratio of offspring tends to be male biased. Female *M. rixator* can be collected from September to November using trap nests with a thicker inner diameter.

Key words leaf-cutter bee; solitary bee; subtropical forest; trap-nest; sex ratio

人类活动引发的环境变化正在改变全球生态系统组成,导致物种灭绝和多个尺度上的生物多样性丧失 (Huang *et al.*, 2018; Isbell *et al.*, 2018; Newbold, 2018; Schuldt *et al.*, 2019)。近年来,全球昆虫种群数量正在不断下降 (Dirzo *et al.*, 2014; Hallmann *et al.*, 2017)。尤其是膜翅目昆虫数量的急剧下降引起了科学界广泛关注 (Garibaldi *et al.*, 2013; Klein *et al.*, 2018)。这是因为该类昆虫在生态系统中不仅能提供传粉和寄生等重要的生态服务功能 (Losey and Vaughan, 2006),而且也可以作为生态环境改变的指示生物 (Tscharntke *et al.*, 1998)。独栖性蜜蜂是农作物和野生植物的关键传粉者,其种群数量的微量下降也会对传粉率产生严重影响 (Kremen *et al.*, 2002)。2006-2007 年,北美地区的西方蜜蜂种群数量经历了一次史无前例的下降 (Stokstad, 2007)。在此背景下,当地的独栖性蜜蜂可以提供一定程度的补充保障,并且对当地作物的授粉做出了很大的贡献 (Holzschuh *et al.*, 2012)。独栖性蜜蜂占蜜蜂种类的 90% 左右,在野生植物和作物授粉中发挥的重要作用不容忽视 (Garibaldi *et al.*, 2013; Zaragoza-Trello *et al.*, 2021)。因此,开展这类功能昆虫群的研究意义重大。

窄切叶蜂 *Megachile rixator* 隶属于膜翅目 Hymenoptera 蜜蜂总科 Apoidea 切叶蜂科 Megachilidae 切叶蜂属 *Megachile*, 分布于我国的北京、浙江、福建、江西、台湾及朝鲜半岛和日本 (何俊华等, 2004; Miyanaga and Maeta, 2013; Guo *et al.*, 2021)。日本地区之前的研究发现窄

切叶蜂使用植物叶片筑巢 (Miyanaga and Maeta, 2013),但是该研究并未报道其它的生物学习性。目前,关于窄切叶蜂相关生物学研究,尤其是筑巢习性方面还很缺乏。

本研究以中国东南部亚热带森林分布的窄切叶蜂为研究对象,调查并分析其筑巢生物学特性,以期为后期开展该蜂的保护、人工管理和驯化提供数据支持,并为更广泛和深入地在亚热带地区开展该类功能昆虫群的筑巢生物学研究奠定基础。

1 材料与方法

1.1 研究地点概况

研究地点位于江西省上饶市德兴市新岗山镇附近的 BEF-China 样地 ($117^{\circ}54'E$, $29^{\circ}07'N$)。实验样地处亚热带,年平均温度 $16.7^{\circ}C$,年平均降雨量 1 821 mm,是典型的亚热带季风气候 (Yang *et al.*, 2013)。

1.2 实验设计

本研究在样地共设计了 88 个采集样方,分别在 2015 年 9 月至 2020 年 8 月观察并收集窄切叶蜂。选用当地芦苇 (长度:20 cm,直径 2-25 mm),并切割成长度为等长 20 cm。将内径为 2-25 mm 不等的芦苇随机混合放入巢箱 (由 Polyvinyl chloride 材料制成),并装满 (图 1: A)。在每个样方 ($7\text{ m} \times 7\text{ m}$) 中心对角线端点上分别放置 2 根距离地面 1.5 m 高的木柱,并将巢箱固定木柱上 (图 1: B)。研究表明朝向会影响筑巢膜翅目

昆虫的筑巢偏好 (Budriene *et al.*, 2004), 因此巢箱的开口方向均设置为东西向。每月月末检查样方, 取走已筑巢的巢管, 并放入新的巢管。

1.3 室内处理

从样方取回的巢管在室内解剖, 记录每个巢管的采集日期、巢口直径、巢室数量以及寄生情况, 并将巢管放置在试管中, 用棉花堵住瓶口, 置于室温下饲养, 直到成虫羽化。然后将成虫制成标本并编号, 记录成虫羽化的时间和性别。

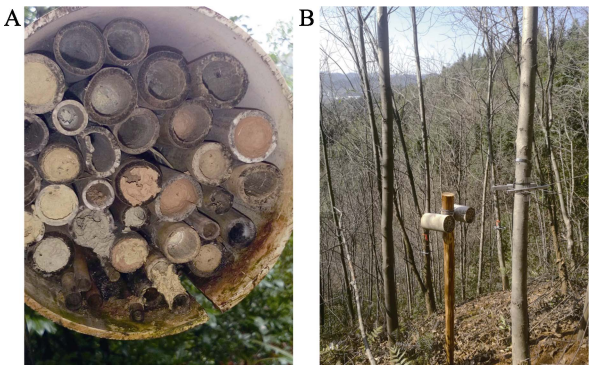


图 1 样方巢管设置
Fig. 1 Trap nest setup in the plot
A. 巢管材料; B. 巢管设置。
A. Trap nest materials; B. Trap nest setups.

1.4 数据分析

实验获得的数据记录在 Excel 2016 表格中, 统计并计算窄切叶蜂的相关生物学数据。在 R 3.4.3 (www.r-project.org) 中的 “ggplot2” 程序包进行作图。

2 结果与分析

2.1 窄切叶蜂的筑巢与被寄生信息汇总

本实验共收集到 199 根窄切叶蜂筑巢的巢管, 巢室数量 866 个。其中成功羽化 347 头成虫, 雄性个体数量为 221, 雌性个体数量为 126; 总体死亡率 60%。目前发现窄切叶蜂被蜂虻 *Anthrax* sp.、厚腹尖腹蜂 *Coelioxys crassiventris*、巨柄啮小蜂 *Melittobia sosui*、疯麻蝇 *Miltogramma* sp. 和长尾小蜂寄生, 寄生率分别为 0.92%、8.60%、

13.60%、0.57%和 0.23%, 总寄生率为 23.90% (表 1)。

表 1 窄切叶蜂的寄生性天敌的寄生信息
Table 1 Information of natural enemy of *Megachile rixator*

科 Family	种 Species	寄生率 (%) Parasitism rate (%)
蜂虻科 Bombyliidae	岩蜂虻属未定名种 <i>Anthrax</i> sp.	0.92
切叶蜂科 Megachilidae	厚腹尖腹蜂 <i>Coelioxys crassiventris</i>	8.60
姬小蜂科 Eulophidae	巨柄啮小蜂 <i>Melittobia sosui</i>	13.60
麻蝇科 Sarcophagidae	蜂麻蝇属未定名种 <i>Miltogramma</i> sp.	0.57
长尾小蜂科 Torymidae	长尾小蜂科未定名种 Torymidae sp.	0.23

2.2 窄切叶蜂的巢室分布与筑巢活动

亲代雌性使用植物叶片封闭巢口和建造巢室, 叶片一层层包裹巢室, 巢室呈线性排列 (图 2); 后代巢室位置按照雌性在内, 雄性在外分布, 并且雌性羽化时间晚于雄性。窄切叶蜂在当年 5-11 月均有筑巢活动发生, 其中 9 月为筑巢高峰期 (图 3: A), 平均每次在一根巢管建造巢室 (4.37±2.59) 个, 每间巢室产下一粒卵。巢口内径分布范围 5-17 mm, 平均巢口内径 (10.00±2.37) mm, 亲代雌性偏向于在巢内径为 11-13 mm 的范围内筑巢 (图 3: B)。亲代雌性当年 9 月以后所产后代会滞育, 以预蛹期越冬, 来年 5 月上旬开始羽化。后代性比在 5 月最高, 之后随月份



图 2 窄切叶蜂巢室分布
Fig. 2 Overview of the cells of *Megachile rixator*

有递减的趋势,但在 11 月性比又有所上升(图 3: C)。后代性比在内径 5-7 mm 范围内最低,随

巢口内径上升而升高,但在内径 13-15 mm 范围内又下降(图 3: D)。

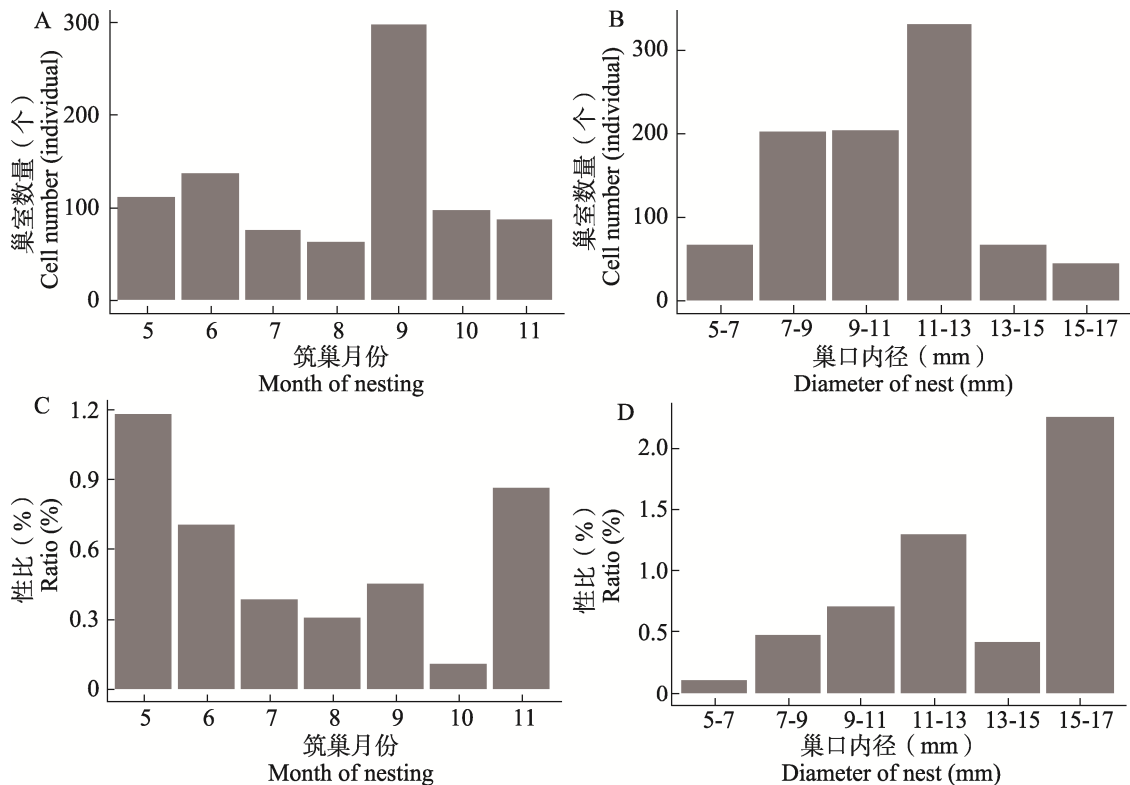


图 3 窄切叶蜂巢室数量与筑巢月份 (A) 和巢口内径 (B) 关系, 以及后代性比与筑巢月份 (C) 和巢口内径 (D) 关系

Fig. 3 The relationships between nesting month (A) and nest diameter (B), and the cell number, nesting month (C), nest diameter (D), and sex ratio of *Megachile rixator*

3 讨论与结论

切叶蜂属 *Megachile* 的其它物种, 如 *M. maculata*、*M. gomphrenoides* 和 *Megachile (Eutricharaea) concinna* 存在较高死亡率的现象, 其死亡率分别为 26%、30%和 34% (Pablo Torretta *et al.*, 2012; Alvarez *et al.*, 2016; Sabino and Antonini, 2017)。研究发现一种尖腹蜂 *Coelioxys* sp. 是 *M. maculate* 的主要天敌, 可导致其 15% 的后代死亡 (Sabino and Antonini, 2017)。虽然本研究也发现一种尖腹蜂 *C. crassiventris*, 但是寄生率并不高, 而巨柄啮小蜂 *M. sosui* 是窄切叶蜂最主要的天敌。我们认为窄切叶蜂的筑巢材料 (植物叶片) 密闭性较差, 是导致其更容易被体型较小的寄生蜂寄生的原因, 如本研究中的

巨柄啮小蜂。

切叶蜂属其它物种也存在后代性比偏向雄性的现象, 如 *M. strupigera* (何波等, 2016)。Rosenheim 等 (1996) 学者提出了“多层面亲代投资”假说来解释这一现象, 即亲代雌性根据资源可用性和卵母细胞可用性来决定其性投资, 以最大限度地提高繁殖成功率 (Seidelmann, 2006)。这种性比偏向现象可能是由于当地资源缺乏, 导致亲代雌性更偏向于产出更多雄性后代。

切叶蜂的筑巢材料丰富, 通常使用植物叶片 (Zillikens and Steiner, 2004; Pablo Torretta *et al.*, 2012)、树脂 (Armbrust, 2004; Pains, 2004; O'Neill and O'Neill, 2016) 和黏土 (Gupta *et al.*, 2004; Pablo Torretta *et al.*, 2014) 等材料筑巢。研究发现切叶蜂属的种类通常将巢室线性排列

(Cardoso and Silveira, 2012; Alqarni *et al.*, 2014), 并且往往也是雌性后代在内, 雄性后代在外 (Scott *et al.*, 2000; O'Neill and O'Neill, 2016)。由于雄性后代早于雌性后代羽化, 这样的性别分配策略可能更有益于后代的存活 (Paini, 2004)。本研究结果也支持这一观点。大多数切叶蜂属种类会在一根巢管内建造多个巢室, 每个巢室产下一个后代 (Pablo Torretta *et al.*, 2012; Alqarni *et al.*, 2014; Sabino and Antonini, 2017)。切叶蜂属的种类呈现不同的化性, 如一化性的 *M. catamarcensis* (Pablo Torretta *et al.*, 2014), 二化性的 *M. pseudanthidioides* (Zillikens and Steiner, 2004) 和海切叶蜂 *M. leachella* (蒙艳华和徐环李, 2007) 以及多化性的 *M. maculata* (Sabino and Antonini, 2017) 和 *M. apicalis* (Kim and Thorp, 2001)。

巢口内径和筑巢蜂类的个体大小有关 (Longair, 1981)。通常筑巢切叶蜂属的雌性个体比雄性个体大 (Kim and Thorp, 2001; O'Neill *et al.*, 2010; Katayama and Matsuda, 2012), 这也解释了为什么窄切叶蜂雌性后代的比例随着巢口内径的上升而升高。然而, 本研究发现在内径 13-15 mm 范围内窄切叶蜂雌性后代的比例骤然下降。这可能是此内径范围的窄切叶蜂雌性后代遭受了更多的寄生性天敌的攻击, 导致其比例下降。研究表明切叶蜂后代的性比偏向与亲代雌性提供食物资源的效率有关 (Kim, 1999; Seidelmann, 2006)。窄切叶蜂偏向于在每年 5 月产出更多雌性后代, 我们认为这可能是由于当地 5 月份很多蜜源植物正值开花季, 亲代雌性可以提供充足的食物来源。窄切叶蜂后代的性比在 11 月又有所上升, 我们认为这可能是为了来年有充足的雌性后代进行交配活动, 从而保证后代的顺利延续。同时, 我们也收集到了窄切叶蜂的花粉。为明确其蜜源植物, 我们将对该蜂的花粉进行进一步分析。

本文对中国东南部亚热带森林的窄切叶蜂的筑巢生物学特性进行观察, 结果发现窄切叶蜂是典型的独栖性切叶蜂, 使用植物叶片建造巢室, 每年从春末到秋末持续发生筑巢活动, 且呈多化性, 每次筑巢会产下多个后代, 后代性比偏向雄性, 且后代死亡率较高。建议在当年 9-11 月 (筑巢率极低) 使用较高内径的人工巢管诱集

窄切叶蜂, 这样可以尽可能地获得更多的雌性后代应用于相关作物的授粉。

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参考文献 (References)

- Alqarni AS, Hannan MA, Gonzalez VH, Engel MS, 2014. Nesting biology of the leafcutting bee *Megachile minutissima* (Hymenoptera: Megachilidae) in central Saudi Arabia. *Annals of the Entomological Society of America*, 107(3): 635–640.
- Alvarez LJ, Lucia M, Aquino DA, Ramello PJ, Abrahamovich AH, 2016. Nesting biology and associated insect enemies of the exotic leaf cutter bee *Megachile (Eutricharaea) concinna* (Hymenoptera: Megachilidae) in Argentina. *Journal of Apicultural Research*, 54(4): 305–313.
- Armbrust EA, 2004. Resource use and nesting behavior of *Megachile prosopidis* and *M. chilopsidis* with notes on *M. discorhina* (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society*, 77(2): 89–98.
- Budriene A, Budrys E, Nevronyte Z, 2004. Solitary Hymenoptera aculeata inhabiting trap-nests in Lithuania: Nesting cavity choice and niche overlap. *Latvijas Entomologs*, 41: 19–31.
- Cardoso CF, Silveira FA, 2012. Nesting biology of two species of *Megachile* (Moureapis) (Hymenoptera: Megachilidae) in a semideciduous forest reserve in southeastern Brazil. *Apidologie*, 43(1): 71–81.
- Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B, 2014. Defaunation in the Anthropocene. *Science*, 345(6195): 401–406.
- Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I, Benjamin F, Boreux V, Cariveau D, Chacoff NP, Dudenhoefter JH, Freitas BM, Ghazoul J, Greenleaf S, Hipolito J, Holzschuh A, Howlett B, Isaacs R, Javorek SK, Kennedy CM, Krewenka KM, Krishnan S, Mandelik Y, Mayfield MM, Motzke I, Munyuli T, Nault BA, Otieno M, Petersen J, Pisanty G, Potts SG, Rader R, Ricketts TH, Rundlof M, Seymour CL, Schuepp C, Szentgyorgyi H, Taki H, Tschamtkke T, Vergara CH, Viana BF, Wanger TC, Westphal C, Williams N, Klein AM, 2013. Wild pollinators enhance fruit set of crops regardless of

- honey bee abundance. *Science*, 339(6127): 1608–1611.
- Guo PF, Wang MQ, Orr M, Li Y, Zhu CD, 2021. Tree diversity promotes predatory wasps and parasitoids but not pollinator bees in a subtropical experimental forest. *Basic and Applied Ecology*, 53(1): 134–142.
- Gupta RK, Naval RK, Charan SK, Rajpurohit A, 2004. Nesting biology of *Megachile (Callomegachile) cephalotes* Smith, a solitary bee that nests in castor sticks (Hymenoptera, Megachilidae). *Mellifera*, 4(8): 21–32, 53–64.
- Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Mueller A, Sumser H, Hoerren T, Goulson D, de Kroon H, 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, 12(10): e0185809.
- He B, Huang DY, Su TJ, Niu ZQ, Gu ZY, Zhu CD, 2016. Bionomics of *Megachile strupigera* Cockerell (Hymenoptera: Megachilidae). *Journal of Environmental Entomology*, 38(6): 1237–1244. [何波, 黄敦元, 苏田娟, 牛泽清, 谷战英, 朱朝东, 2016. 白斑切叶蜂的生物学特性观察. 环境昆虫学报, 38(6): 1237–1244.]
- He JH, 2004. Hymenopteran Insect Fauna. Beijing: Science Press. 1026. [何俊华, 2004. 浙江蜂类志. 北京: 科学出版社. 1026.]
- Holzschuh A, Dudenhoefter JH, Tschardt T, 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biological Conservation*, 153: 101–107.
- Huang Y, Chen Y, Castro-Izaguirre N, Baruffol M, Brezzi M, Lang A, Li Y, Haerdle W, von Oheimb G, Yang X, Liu X, Pei K, Both S, Yang B, Eichenberg D, Assmann T, Bauhus J, Behrens T, Buscot F, Chen XY, Chesters D, Ding BY, Durka W, Erfmeier A, Fang J, Fischer M, Guo LD, Guo D, Gutknecht JLM, He JS, He CL, Hector A, Hoenig L, Hu RY, Klein AM, Kuehn P, Liang Y, Li S, Michalski S, Scherer-Lorenzen M, Schmidt K, Scholten T, Schuldt A, Shi X, Tan MZ, Tang Z, Trogisch S, Wang Z, Welk E, Wirth C, Wubet T, Xiang W, Yu M, Yu XD, Zhang J, Zhang S, Zhang N, Zhou HZ, Zhu CD, Zhu L, Bruelheide H, Ma K, Niklaus PA, Schmid B, 2018. Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science*, 362(6410): 80–83.
- Isbell F, Cowles J, Dee LE, Loreau M, Reich PB, Gonzalez A, Hector A, Schmid B, 2018. Quantifying effects of biodiversity on ecosystem functioning across times and places. *Ecology Letters*, 21(6): 763–778.
- Katayama E, Matsuda T, 2012. Nesting biology and nest architecture of the Japanese leaf-cutting bee *Megachile kyotensis* Alfken (Hymenoptera, Megachilidae). *Japanese Journal of Entomology New Series*, 15(3): 159–171.
- Kim JY, 1999. Influence of resource level on maternal investment in a leaf-cutter bee (Hymenoptera: Megachilidae). *Behavioral Ecology*, 10(5): 552–556.
- Kim JY, Thorp RW, 2001. Maternal investment and size-number trade-off in a bee, *Megachile apicalis*, in seasonal environments. *Oecologia*, 126(3): 451–456.
- Klein AM, Boreux V, Fornoff F, Mupepele AC, Pufal G, 2018. Relevance of wild and managed bees for human well-being. *Current Opinion in Insect Science*, 26: 82–88.
- Kremen C, Williams NM, Thorp RW, 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America*, 99(26): 16812–16816.
- Longair RW, 1981. Sex-ratio variations in xylophilous aculeate Hymenoptera. *Evolution*, 35(3): 597–600.
- Losey JE, Vaughan M, 2006. The economic value of ecological services provided by insects. *Bioscience*, 56(4): 311–323.
- Meng YH, Xu HL, 2007. Nesting and foraging behavior of *Megachile maritima* (Hymenoptera: Megachilidae). *Acta Entomologica Sinica*, 50(12): 1247–1254. [蒙艳华, 徐环李, 2007. 海切叶蜂的筑巢和访花行为. 昆虫学报(12): 1247–1254.]
- Miyanaga R, Maeta Y, 2013. A newly found nesting site of *Megachile rixator sakishimana* Yasumatsu et Hirashima in Iriomote Island, Southernmost Archipelago, Japan (Hymenoptera, Megachilidae). *New Entomologist*, 57(2): 1–4.
- Newbold T, 2018. Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society B-Biological Sciences*, 285 (1881): 1–9.
- O'Neill KM, Pearce AM, O'Neill RP, Miller RS, 2010. Offspring size and sex ratio variation in a feral population of alfalfa leafcutting bees (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America*, 103(5): 775–784.
- O'Neill KM, O'Neill JF, 2016. Brood parasitism of the resin bee *Megachile campanulae* (Robertson) by *Coelioxys modesta* Smith (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society*, 89(2): 117–127.
- Pablo Torretta J, Patricia Durante S, Guadalupe Colombo M, Mabel Basilio A, 2012. Nesting biology of the leafcutting bee *Megachile (Pseudocentron) gomphrenoides* (Hymenoptera: Megachilidae) in an agro-ecosystem. *Apidologie*, 43(6): 624–633.
- Pablo Torretta J, Patricia Durante S, Mabel Basilio A, 2014. Nesting ecology of *Megachile (Chrysosarus) catamarcensis* Schrottkey

- (Hymenoptera: Megachilidae), a prosopis-specialist bee. *Journal of Apicultural Research*, 53(5): 590–598.
- Paini DR, 2004. Nesting biology of an Australian resin bee (*Megachile* sp.; Hymenoptera: Megachilidae): A study using trap nests. *Australian Journal of Entomology*, 43: 10–15.
- Rosenheim JA, Nonacs P, Mangel M, 1996. Sex ratios and multifaceted parental investment. *American Naturalist*, 148(3): 501–535.
- Sabino WDO, Antonini Y, 2017. Nest architecture, life cycle, and natural enemies of the neotropical leafcutting bee *Megachile (Moureapis) maculata* (Hymenoptera: Megachilidae) in a montane forest. *Apidologie*, 48(4): 450–460.
- Schuldt A, Ebeling A, Kunz M, Staab M, Guimaraes-Steinicke C, Bachmann D, Buchmann N, Durka W, Fichtner A, Fornoff F, Haerdtle W, Hertzog LR, Klein AM, Roscher C, Schaller J, von Oheimb G, Weigelt A, Weisser W, Wirth C, Zhang J, Bruehlheide H, Eisenhauer N, 2019. Multiple plant diversity components drive consumer communities across ecosystems. *Nature Communications*, 10: 1–11.
- Scott VL, Kelley ST, Strickler K, 2000. Reproductive biology of two *Coelioxys* cleptoparasites in relation to their *Megachile* hosts (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America*, 93(4): 941–948.
- Seidelmann K, 2006. Open-cell parasitism shapes maternal investment patterns in the red mason bee *Osmia rufa*. *Behavioral Ecology*, 17(5): 839–848.
- Stokstad E, 2007. Genomics - Puzzling decline of US bees linked to virus from Australia. *Science*, 317(5843): 1304–1305.
- Tscharntke T, Gathmann A, Steffan-Dewenter I, 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: Community structure and interactions. *Journal of Applied Ecology*, 35(5): 708–719.
- Yang X, Bauhus J, Both S, Fang T, Haerdtle W, Kroeber W, Ma K, Nadrowski K, Pei K, Scherer-Lorenzen M, Scholten T, Seidler G, Schmid B, von Oheimb G, Bruehlheide H, 2013. Establishment success in a forest biodiversity and ecosystem functioning experiment in subtropical China (BEF-China). *European Journal of Forest Research*, 132(4): 593–606.
- Zaragoza-Trello C, Vila M, Bartomeus I, 2021. Interaction between warming and landscape foraging resource availability on solitary bee reproduction. *Journal of Animal Ecology*, 90(11): 2536–2546.
- Zillikens A, Steiner J, 2004. Nest architecture, life cycle and cleptoparasite of the neotropical leaf-cutting bee *Megachile (Chrysosarus) pseudanthidioides* Moure (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society*, 77(3): 193–202.