



壁蜂生物学特性与传粉服务功能*

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摘要 壁蜂是对蜜蜂总科 (Apoidae) 切叶蜂科 (Megachilidae) 壁蜂属 (*Osmia*) 的统称, 主要分布北半球的温带区域, 在自然生态系统和农田生态系统中均发挥着重要的传粉生态服务功能。壁蜂群居筑巢、接受人类提供的巢穴、一年一代的习性, 使它们很容易被大量饲养, 并且人们可以通过调节其在春节破茧羽化的时间与作物花期同步, 为多种目标作物授粉。本文综述壁蜂的生物学和生态学特性、传粉功能及其影响因子, 旨在为发挥壁蜂的传粉功能提供参考。

关键词 壁蜂, 生物学特性, 作物, 传粉功能, 影响因素

Biological characteristics and pollination service of Mason bee

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Abstract Mason bee is a name commonly used for species of bees in the genus *Osmia*, of the family Megachilidae, of the super family Apoidae. Mason bee most occurs in the temperate regions of the Northern Hemisphere, holding the important pollination services in both agricultural and natural environments. The gregarious nesting behaviour of these solitary bees, their acceptance of a variety of different man-made nesting materials and univoltine are important properties for successful mass rearing. Their emerging time can be optimized to synchronize the blooming time of crops, so they can be used to pollinate different crops. Biology, ecology, pollination service of mason bee and the influence factors are reviewed.

Key words *Osmia*, biological characteristics, crops, pollination service

世界上主要农作物中 85%都依赖于蜜蜂等昆虫授粉 (Klein *et al.*, 2007; Ollerton *et al.*, 2011)。近年来, 全球传粉昆虫种群下降, 不仅导致了自然传粉作用不足, 而且给农业造成了巨大的经济损失 (Potts *et al.*, 2010), 这一问题随着意大利蜜蜂 *Apis mellifera* L. 种群在北美和欧洲突然减少, 被进一步放大。蜜蜂的减少促使人们寻找解决方案, 而壁蜂就是一种非常重要的替代传粉昆虫 (Sheffield *et al.*, 2008)。壁蜂是对

蜜蜂总科 (Apoidae) 切叶蜂科 (Megachilidae) 壁蜂属 (*Osmia*) 的统称, 因其利用泥土等材料在墙壁的缝隙、孔洞中筑巢而得名。目前, 发现的壁蜂有 300 多种, 主要分布北半球的温带区域, 具有重要的传粉生态服务功能 (Adamson *et al.*, 2012; Holzschuh *et al.*, 2012; Brittain *et al.*, 2013; Garibaldi *et al.*, 2013)。壁蜂与蜜蜂一样是单倍二倍体遗传系统, 但是社会行为和生活史与蜜蜂截然不同。群居筑巢、一年一代、容易在

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人造巢穴中营巢的习性,使它们很容易大量饲养,并且人们可以通过调节其出巢时间,为多种目标作物授粉(Torchio, 1976)。壁蜂可以为苹果、梨、草莓、樱桃、三叶草等多种农作物授粉,提升农作物的产量和质量。因其优良的传粉特性,全世界已经有多种壁蜂被人工繁殖并应用于作物授粉,主要包括蓝壁蜂 *O. lignaria*、红壁蜂 *O. rufa*、欧洲壁蜂 *O. cornuta*、角额壁蜂 *O. cornifrons*、蓝莓壁蜂 *O. ribifloris*、凹唇壁蜂 *O. excavata*、紫壁蜂 *O. jacoti* 等。我国农业生产中广泛应用的壁蜂是凹唇壁蜂、角额壁蜂。本文对壁蜂的生物学特性、传粉功能及其影响因子进行了综述,旨在为发挥壁蜂的传粉功能提供参考。

1 壁蜂的生物学特性

1.1 壁蜂的生活史

壁蜂每年发生 1 代,巢外活动的时间主要在春季和初夏。在春季,壁蜂破茧而出,进行交配、采集花粉、筑巢产卵。卵一周后开始孵化,受精卵发育成雌蜂,而未受精卵发育成雄蜂(Elias *et al.*, 2010)。卵孵化后一个月后开始结茧,大约 56 d 后化蛹,保持蛹期大约 50 d,随后羽化成虫(Raw, 1972)。成虫在茧中滞育越冬,直到春季出巢。一般雄虫排列在巢管的前端,因此雄虫先出巢,雌虫后出巢。雌蜂交配后,采集花粉、筑巢产卵。雌蜂将花粉和少量花蜜混合成湿润的花粉团,作为幼虫的食物。

1.2 交尾繁殖

在交尾繁殖期,有些雄蜂在靠近蜂巢的地方建立领地,有些则在开花的区域等待、追求雌蜂、伺机交尾(Raw and O'Toole, 1979; Siedelmann, 1999)。当雄蜂发现可以交尾的雌蜂时,会竞相与之交配,但是一般不会相互袭击。雌蜂主要通过感知雄蜂胸部震动,评价雄蜂的健康和适合度(Conrad *et al.*, 2010; Conrad and Ayasse, 2015)。雌蜂通常只与一只雄蜂交尾,例如,雄性红壁蜂在与雌性红壁蜂交配时,在其交配囊中形成交配

塞,保证了第一次交配的精子的受精率,符合雄性高竞争和低交配率的行为(Seidelmann, 2015)。

1.3 滞育越冬

壁蜂是典型一化性昆虫,其滞育不依赖于光周期,滞育持续时间主要受温度的影响,保幼激素对滞育解除发挥了重要的作用(Wasielewski *et al.*, 2011)。红壁蜂从 11 月开始滞育,1 月底打破滞育,滞育期持续 100 多天,滞育有助于壁蜂度过冬季严寒(Dmochowska *et al.*, 2013)。越冬期间红壁蜂的卵巢并不完全停止活跃,卵母细胞继续发育(Wasielewski *et al.*, 2011)。壁蜂越冬包括滞育和滞育后两个阶段,在滞育阶段壁蜂的过冷却点降低(Krunić and Stanisavljević, 2006),有助于壁蜂耐受冬季低温,但是滞育壁蜂在 20℃ 下会死亡。滞育后阶段恢复发育,其发育受到温度变化影响和抑制(Bosch *et al.*, 2010),因此在滞育后阶段,壁蜂可以在低温下保存很长一段时间,人们可以利用该特点控制释放壁蜂的时间。延长壁蜂滞育后的时间不仅导致储存的能量物质过度消耗,而且会使抗氧化系统的功能部分损失(Dmochowska *et al.*, 2012),从而对壁蜂的存活和繁殖产生不利影响(Bosch and Blas, 1994; Bosch and Kemp, 2003, 2004)。Wasielewski 等(2013)研究了成虫在茧中的新陈代谢过程,解析了其成功越冬的新陈代谢策略。与以幼虫或蛹越冬的蜂种相比,壁蜂在应对全球气候变暖环境时,表现出不同的代谢策略(Fründ *et al.*, 2013)。

1.4 食物和觅食

采集食物和筑巢占据了壁蜂 85%-90% 的活动时间,雌蜂需要来回飞行几十次才能完成一个巢室(Zurbuchen *et al.*, 2010)。雌壁蜂为后代准备的花粉团主要由花粉和少量花蜜构成,壁蜂可以采集多种花粉(Teper and Biliński, 2009),雌壁蜂喜欢采集花粉多的花朵,花粉的多样性对壁蜂后代的生长发育没有影响(Radmacher and Strohm, 2010)。红壁蜂拥有三色视觉系统,帮助其从花丛中寻找花粉(Menzel *et al.*, 1988)。

2 壁蜂的传粉功能

蜜蜂是比较全面的传粉昆虫,可以为很多种植物传粉,但是其对一些作物(例如蓝莓、番茄、马铃薯等)传粉效率差。设施蔬菜应用蜜蜂授粉也困难重重,因为蜜蜂在密闭的温室中,会迷失方向,发生撞棚现象(吴翠翠等,2016)。特别是近年来全球的“蜂群衰竭失调症”(CCD),促使人们寻找一些替代蜂种补足农田生态系统中作物授粉需求。壁蜂成为应用最为广泛的替代蜂种,特别对果树授粉。壁蜂广泛分布于世界各地,耐低温、访花效率高,尤其是用腹部的腹毛刷采集携带花粉,对苹果等果树的授粉效率远远高于蜜蜂。人们很早就开始了其生物学和传粉生态学研究(Torchio,1987),上个世纪40年代日本将角额壁蜂成功应用于果树授粉,此后蓝壁蜂 *O. lignaria*、欧洲壁蜂 *O. cornuta*、红壁蜂 *O. rufa* 被应用于为蔷薇科果树(苹果、桃、梨、杏、李、樱桃、扁桃、酸樱桃)授粉(Torchio,1976,1985; Corliss,1992; Bosch *et al.*,2000; Bosch and Kemp,2001)。蓝莓壁蜂在美国被成功的应用于为杜鹃花科的蓝莓授粉(Torchio,1990; Sampson and Cane,2000; Sampson *et al.*,2004)。

角额壁蜂 *O. cornifrons* 起源于东亚地区,为苹果授粉的效率比意大利蜜蜂高80多倍(Maeta and Kitamura,1981)。20世纪40年代在日本被驯化,目前日本75%以上的苹果园应用角额壁蜂授粉(Bosch and Kemp,2001)。1977年被美国农业部引入美国东北部(Torchio *et al.*,1987),现在美国西北果区也有分布(Batra,1978)。我国于1987年从日本引入角额壁蜂(魏枢阁和王韧,1990),在应用过程中逐渐被当地的凹唇壁蜂替代。角额壁蜂一年的巢外活动时间为4月到6月,大约6-8周。角额壁蜂的活跃水平受到时间、温度和降雨的影响,13.9℃即开始后活动,一般其活动时间从早上的8:00到晚上8:00(Matsumoto and Maejima,2010),活跃度随着温度上升而增加,在雨天角额壁蜂基本上不外出采集花粉。角额壁蜂完成一个巢室平均需要31.3次飞行,需要290余次飞行完成一个蜂管(平均

每个巢管有9.5个巢室)(McKinney and Park,2012)。

蓝壁蜂 *O. lignaria* 主要分布在北美洲(Torchio,1976; Bosch and Kemp,2001),一年的巢外活动时间为3月到6月,可以采集的多种花粉(包括紫荆、草莓、天竺葵、苹果、李、柳、蒲公英等),主要用来给苹果、桃、樱桃、扁桃和蓝莓授粉(Torchio,1981; Bosch and Kemp,1999)。在野外温度高于14℃时,蓝壁蜂破茧而出。雌壁蜂体长14mm,雄壁蜂体长11mm。蓝壁蜂完成一个巢室需要32.4次飞行,其中建筑一个泥壁需要6.9次飞行(Phillips and Klostermeyer,1978),每个巢管约有3.64个巢室,一般有2-3个雌蜂,1-2个雄蜂(Torchio,1976)。

红壁蜂 *O. bicornis* 起源于欧洲(Krunić and Stanisavljević,2006),主要在分布在欧洲和西亚地区,野外在树干、空虫洞、蜗牛壳等处筑巢。红壁蜂的雌雄个体差异明显,雌性体长10-12mm,雄性体长8-10mm,雌性体重是雄性的1.6倍(Raw,1972; Ingolf,2004)。雌蜂在每个巢管中平均建造6个巢室,大个体建造的巢室更多(Karsten *et al.*,2010)。红壁蜂的最大觅食距离为600m(Gathmann and Tscharrnke,2002)。红壁蜂是优良的授粉昆虫,性情比蜜蜂温顺,一般不会蜇人,在欧洲被广泛用于苹果、草莓、油菜等作物授粉(Holm 1974; Teper and Biliński,2009; Gruber *et al.*,2011)。

凹唇壁蜂 *O. excavata* 主要分布于东亚地区,是我国北方的一个野生传粉昆虫,1990年被发现并用于给苹果树授粉(吕家睦等,1992)。作为本土物种,其适应我国北方果区气候,与果树形成了长期协同关系,具有耐冬季低温(魏永平等,2001)、发育起点温度低、日传粉活动时间长、访花频率快(杨龙龙等,1997a,1997b)、授粉效率高、饲养管理简便的优点(魏永平等,2000),其授粉效果好于蜜蜂、人工授粉及其他壁蜂(吕家睦等,1993;何伟志和周伟儒,2009)。凹唇壁蜂授粉能显著提高坐果率,增加单果重

量、提高果品产量和质量、增加果实抗病能力,使果型端正(孙建设等,1999;龚声信等,2008;魏树伟等,2012;王贵平等,2013)。因而,凹唇壁蜂被称为传粉之王,成为我国的重要的传粉资源昆虫(Zhang *et al.*, 2008; Winfree, 2010),已被人工饲养并广泛应用于给苹果、梨、桃、樱桃等北方常栽果树传粉在我国水果生产中发挥着重要的传粉生态服务功能(刘新生和魏枢阁,1997; Wei *et al.*, 2002; 王凤鹤和杨甫,2007)。近年来,凹唇壁蜂的传粉功能被不断的挖掘,被用于全国各地蔬菜、瓜类等作物授粉增产和制种,其在巢穴周围 100 m 范围内活动的习性有利于定点授粉,非常适合我国当前的一家一户小面积作物授粉(丁楠等,2013)。

3 影响壁蜂种群和传粉功能的因素

应用壁蜂为作物授粉,不仅要关注提高其授粉效率,而且要充分考虑壁蜂的生物学和生态学特点,通过合理的管理获得持续和健康的壁蜂种群。影响壁蜂种群的因子主要包括壁蜂筑巢材料、释放方法、环境胁迫因子、壁蜂发育与作物开花不一致性、蜜粉源缺乏、化学农药、自然天敌等(Sedivy and Dorn, 2014; 曹衍斌等,2017; 刘丽等,2018; 袁锐等,2018)。

3.1 筑巢活动

环境气候因子对壁蜂种群的影响非常大。例如,在最适宜环境下,欧洲壁蜂的雌蜂能在 4 周内产 30 多个卵,而在农田环境中,其产卵量就会大大下降(Torchio *et al.*, 1987)。低温、刮风和下雨天气均能干扰壁蜂的筑巢和采集行为,而且春季低温会延缓果树开花时间,进而缩短花期,影响壁蜂采集花粉和蜂蜜的时间(Torchio, 1981)。

雌蜂个体大小是影响壁蜂繁殖量的重要生物因子,大个体雌蜂越冬存活率高、筑巢率大、采集效率高、产卵量多、存活时间长(Tepedino and Torchio, 1982; Bosch and Kemp, 2004; Bosch and Vicens, 2006; Seidelmann *et al.*, 2010),且大个体雌蜂能够繁殖个体更大的下一代(Bosch

and Vicens, 2006),雌蜂个体大小与上一代雌蜂采集花粉团的大小和质量密切相关(Bosch and Vicens, 2006; Radmacher and Strohm, 2010; Sedivy *et al.*, 2011)。

蜂巢作为壁蜂的产卵和越冬场所,能够影响壁蜂种群重量和存活。目前生产中常用的壁蜂蜂巢的制作材料有木材、泡沫、纸板、纸管、芦苇管、竹管等(Bosch and Kemp, 2001; Krunic and Stanisavljevic, 2006a)。不同的壁蜂种类对不同材质的蜂巢的选择也不完全相同,木质蜂巢往往比其他蜂巢更有吸引力(Bosch, 1995),而红壁蜂似乎更喜欢芦苇管,虽然其在木质巢穴中发育更好、存活率更高,因此选择蜂巢材料时应综合考虑对壁蜂的吸引力和存活的影响。与新巢管相比,壁蜂有时更喜欢在出生的巢管中筑巢,可能被蜂茧挥发的化学气味吸引(Pitts-Singer, 2007)。壁蜂在旧蜂管筑巢行为会增加后代壁蜂被疾病和蜂螨感染寄生的几率,从而危及壁蜂的生长发育。巢管的长度和孔径也会对壁蜂行为和生长行为产生影响(Bosch and Kemp, 2001)。一般来说,长且孔大的巢穴会有吸引更多的雌蜂、后代死亡率更低、后代个体更大的,但是如果孔径太大,则会失去对壁蜂的吸引力。

蜂箱可以使蜂巢避免阳光曝晒和雨水淋湿,也可以阻止鸟类等天敌的捕食。蜂箱要放在背风向阳的地方,有利于壁蜂尽快出巢活动(Bosch and Kemp, 2001)。同时,壁蜂蜂箱位置要远离地面,避免蚂蚁等天敌的危害(Krunic and Stanisavljevic, 2006a)。壁蜂筑巢需要湿润的泥土来分隔巢室和堵塞巢管,因此在蜂箱附近准备充足的湿润泥土可以提高壁蜂营巢效率(Bosch and Kemp 2001; Krunic and Stanisavljevic, 2006a)。

3.2 释放壁蜂

壁蜂既可以从蜂管中直接释放,也可以将蜂茧收集后一起释放。从蜂管中直接释放,壁蜂在释放地点营巢的比率高达 60%-75%(Bosch and Kemp, 2002),但是这种释放方法可能不利于控制寄生虫和病菌。将收集后的蜂茧一起释放,在

释放前检查去除病蜂和寄生虫,可以有效减少蜂病传播。

壁蜂是非常高效的果园授粉昆虫,根据授粉的果树种类、树龄,一般每公顷释放 350-750 头雌蜂,不可释放过量 (Vicens and Bosch, 2000; Bosch and Kemp, 2004), 过量释放会导致壁蜂筑巢前飞离扩散,而且会增加个体间对于花粉的过度竞争,从而影响壁蜂种群质量和种群增长 (Torchio, 1985)。由于壁蜂可以采集和取食多种植物的花粉 (Haider *et al.*, 2013), 因此在果树开花前,为壁蜂提供替代蜜粉源植物,有助于在果树开花时,壁蜂的传粉效率达到最高,从而提高为果树的传粉功能。集中开花的作物能够提供大量的花蜜和花粉,能够抵消农田生态系统中传粉者下降的作用,例如红壁蜂受益于集中开花的油菜田 (Jauker *et al.*, 2012)。

壁蜂的采集花粉和蜂蜜的距离大约 50-150 m, 远低于蜜蜂的飞行距离,壁蜂出巢取食蜂蜜后,飞行距离、飞行时间、最大飞行速度均有提高 (丁楠等, 2013)。壁蜂蜂箱在果园分布的距离宜在 50-100 m (Krunić and Stanisavljević, 2006a)。壁蜂开始营巢后,就会与营巢位置及周边的视觉地标建立很强的联系,如果移动巢箱,雌蜂很容易被干扰,弃巢离开 (Bosch and Kemp, 2001)。

3.3 壁蜂病虫害

壁蜂病虫害主要包括盗寄生虫 (鞘翅目、蜚蠊目、膜翅目)、寄生虫 (膜翅目、双翅目)、捕食性天敌 (蚂蚁、鸟类、鼠类) 和病原菌 (白垩病)。盗寄生虫取食巢室中蜂粮-花粉团,减少了幼虫的食物,从而使幼虫的体型变小和适应性降低,甚至导致壁蜂幼虫死亡。营盗寄生的蜂螨是壁蜂大量饲养过程中经常遇到问题 (Yamada, 1990; 翟浩等, 2015; 曹衍斌等, 2017)。危害我国凹唇壁蜂的蜂螨主要是平岛氏毛爪螨 (*Chaetodactylus hirashimai* Kurosa), 通过成年蜂携带进入巢管中,取食巢室中的蜂粮-花粉团,繁殖速度很快,使壁蜂的幼虫的饥饿而死 (曹衍斌等, 2017)。该蜂螨不会寄生危害蜂茧和成蜂,

但是其会大量附着在破茧而出的成年蜂体表,进行传播,影响了蜂的活动、采集花粉和传粉的效率。通过清除蜂茧表面的蜂螨、化学或者加热处理壁蜂蜂管能是有效的治螨措施 (周仙红等, 2017)。一些寄生性害虫,例如寄生蜂 (*Monodontomerus* spp.) 将产卵器插入壁蜂蜂茧产卵,危害茧中的壁蜂,一年发生 2-4 代,很难被发现。可以通过在茧上覆盖锯末,黑光灯诱杀成蜂等方法,减少寄生蜂危害。白垩病是球囊菌属真菌侵染壁蜂幼虫引起的重要病害 (Rust and Torchio, 1991), 通过清除发病幼虫,清理和消毒饲养器具可以有效的减少白垩病的发生危害。叉唇寡毛土蜂 *Sapyga coma* Yasumatsu *et* Sugihara 是一种常见的凹唇壁蜂和角额壁蜂捕食性天敌,其对凹唇壁蜂的捕食现象在山东省很普遍,捕食率不同地区有差异,可能与其环境中叉唇寡毛土蜂的虫源数量有关 (刘丽等, 2018)。花斑皮蠹 *Trogoderma variabile* Ballion 是一种适应性强的储藏物害虫,其也会危害蜂管中的壁蜂 (刘丽等, 2018)。

3.4 壁蜂出巢时间

调节壁蜂在果园花期中破茧出巢时间对于壁蜂的繁殖和果树授粉座果都非常重要 (Bosch and Blas, 1994; Bosch *et al.* 2000; Bosch and Kemp, 2004)。如果出蜂早于果树开花,壁蜂会离开果园去寻找新的蜜源;如果出蜂晚于初花期,不仅早期的花就错过了授粉,而且会缩短壁蜂采集花粉和筑巢的时间,从而减少繁殖数量。理想的状况是雌蜂的出巢期与果园初花同步,这要求监测花蕾的发育进度,并结合天气预报尽量准确的预测花期。

决定壁蜂发育和出巢时间的主要因子是发育期的温度。温度对发育速度和发育期的死亡率均有显著影响 (Radmacher and Strohm, 2011)。蓝壁蜂发育时间和死亡率均随着温度升高而上升 (Bosch and Kemp, 2001)。在变温条件下,发育时间比恒温条件下更短,且死亡率更低。在预蛹期,壁蜂处在滞育状态,在这一阶段,其对高温的敏感性最低 (Radmacher and Strohm,

2011), 在这一阶段壁蜂的耗氧量比幼虫期和蛹期大大降低 (Sgolastra *et al.*, 2011)。来自不同气候区壁蜂的预蛹期的时间差异十分明显, 提示我们从其他地区引种壁蜂, 需要避免壁蜂到达新地区不适当地的物候期 (Sgolastra *et al.*, 2012)。

在越冬前期, 壁蜂羽化, 新陈代谢率增加, 此阶段壁蜂是最敏感时期, 很容易死亡 (Bosch and Kemp, 2001; Monzon *et al.*, 2004)。如果越冬前期成虫在较高的温度下时间过长, 身体储存的脂肪等能量物质就会消耗殆尽, 从而导致越冬死亡率增加、成虫无法咬破蜂茧或者没有飞行的能量 (Bosch and Kemp, 2004; Monzon *et al.*, 2004; Bosch *et al.*, 2010; Radmacher and Strohm, 2011; Sgolastra *et al.*, 2011)。越冬前缩短会延长越冬期, 从而导致出巢前期提前和出巢期缩短, 而出巢期是调节壁蜂释放的关键时期 (Bosch and Kemp, 2004)。

越冬期持续时间和环境温度都会直接影响出巢前期和出巢期以及越冬存活率。总的来说, 越冬期增长会缩短出巢前期时间和出巢期时间, 而出巢前期和出巢期时间是调节壁蜂出巢和果树开花同步的关键阶段; 缩短越冬期会延长出巢前期和出巢期的时间 (Bosch *et al.*, 2000)。如果要利用非本地的壁蜂种类, 可将壁蜂转移到可控温条件下, 调节壁蜂的越冬前期和越冬期的温度, 从而使壁蜂出巢和果园开花同步。经过暖冬, 壁蜂会提前出巢, 例如蓝壁蜂在 7 越冬, 比 4 出巢时间缩短一半 (Bosch *et al.*, 2000), 如果壁蜂被置于更高的温度下越冬, 其死亡率升高, 繁殖后代成功率降低 (Bosch and Blas, 1994)。

在自然环境下, 春季温度上升后, 壁蜂就会出巢。利用人工调节温度培养, 可以调节缩短出巢前期的时间, 从而使壁蜂出巢期与目标作物的开花期同步 (Bosch and Kemp, 2001; White *et al.*, 2009)。缩短出巢前期的时间不仅有助于出巢期与开花期同步, 而且能增加壁蜂筑巢成功率。总的来说, 人工调控的温度越高, 壁蜂出巢的时间越短, 如果温度太高, 一些壁蜂就无法出巢 (Bosch

and Kemp, 2001)。

3.5 种群退化

比较研究显示野生角额壁蜂的生活力显著高于果园人工饲养角额壁蜂, 无论是出茧率和繁殖率差异显著, 表明由于人工饲养种群的近亲繁殖、食物资源的单一化造成了种群退化, 影响了壁蜂的授粉功能 (金大勇和吕石龙, 2007)。因此, 在人工饲养壁蜂时, 注意保护和利用当地野生壁蜂种群, 对人工种群进行复壮。

4 化学农药对壁蜂的威胁

化学农药对蜜蜂及其传粉功能的威胁引起了全球关注 (Potts *et al.*, 2010)。最近的大数据研究比较了各种蜜蜂对农药的敏感性, 提示需要对包括壁蜂在内的蜜蜂类群进行农药风险评估 (Arena and Sgolastra, 2014)。烟碱类农药已经被证实是降低蜜蜂等授粉昆虫多样性的重要因子 (Maini *et al.*, 2010; Lundin *et al.*, 2015; Pisa *et al.*, 2015), 三类传粉蜂 (蜜蜂、熊蜂和壁蜂) 中, 壁蜂对烟碱类农药最敏感 (Sgolastra *et al.*, 2016)。烟碱类农药对壁蜂的影响逐渐得到大家的重视, Heimbach 等 (2016) 开展了在大的景观尺度下, 监测噻虫胺包衣油菜对蜜蜂、熊蜂和壁蜂的影响。袁锐等 (2018) 分别采用饲喂法和接触法测定了 6 种新烟碱类杀虫剂对凹唇壁蜂毒性, 发现 6 种新烟碱类杀虫剂对凹唇壁蜂雌成蜂的毒性均为高毒, 对凹唇壁蜂有较高的生态风险性。

5 总结与展望

壁蜂是一类非常有价值的传粉昆虫, 对于维持植物多样性有非常重要的意义。通过人工驯化和饲养, 利用其为果树等作物授粉, 可以替代人工授粉, 达到节约劳动力和增产增收。相对于蜜蜂, 我们对壁蜂的研究处于起步阶段, 为了更好的发挥壁蜂在我国传粉生态服务功能, 建议我国科研工作者从以下几个方面重点突破: (1) 开展壁蜂资源的调查、保护和发掘利用。需要对我国

壁蜂种类和分布进行系统调查,并对不同壁蜂生物学、生态学以及传粉利用价值进行评估。鉴于壁蜂一年发生 1 代,往往与当地的物候期和植物种类协同进化,因此当地的壁蜂更容易适应环境和发挥传粉功能。例如,凹唇壁蜂就是从日本引种、使用角额壁蜂的过程中,逐渐替代角额壁蜂的优异传粉昆虫,其适宜在山东省胶东地区繁殖,虽然被运往全国各地为作物授粉,但是很难在异地繁殖种群。(2)加大对已经发现的角额壁蜂、凹唇壁蜂、紫壁蜂 *O. jocoti* Cockerell、叉壁蜂 *O. pedicornis* Cockerell、壮壁蜂 *O. taurs* Smith 生物学、饲养、授粉应用等研究力度。(3)借鉴国外成熟的蜜蜂授粉对农业价值的方法,并结合我国国情,评估生产上壁蜂传粉功能的功能量、服务价值。(4)研究解决限制壁蜂种群的关键因子,建立壁蜂规模饲养技术,拓展其在农业生产中的传粉增产功能。

参考文献 (References)

- Adamson NL, Roulston TH, Fell RD, Mullins DE, 2012. From April to August-wild bees pollinating crops through the growing season in Virginia. USA. *Environmental Entomology*, 41(4): 813–821.
- Arena M, Sgolastra F, 2014. A meta-analysis comparing the sensitivity of bees to pesticides. *Ecotoxicology*, 23(3): 324–334.
- Batra SWT, 1978. *Osmia cornifrons* and *Pithitis smaragdula*, two Asian bees introduced into the United States for crop pollination// Proceedings of the 6th International Symposium on Pollination. Maryland Agricultural Experiment Station Special Miscellaneous Publication 1. 307–312.
- Bosch J, 1995. Comparison of nesting materials for the orchard pollinator *Osmia cornuta* (Hymenoptera, Megachilidae). *Entomologia generalis*, 19(4): 285–289.
- Bosch J, Blas M, 1994. Effect of over-wintering and incubation temperatures on adult emergence in *Osmia cornuta* Latr (Hymenoptera, Megachilidae). *Apidologie*, 25(3): 265–277.
- Bosch J, Sgolastra F, Kemp WP, 2010. Timing of eclosion affects diapause development, fat body consumption and longevity in *Osmia lignaria*, a univoltine, adult-wintering solitary bee. *Journal of Insect Physiology*, 56(12): 1949–1957.
- Bosch J, Kemp WP, 1999. Exceptional cherry production in an orchard pollinated with blue orchard bees. *Bee World*, 80(4): 163–173.
- Bosch J, Kemp WP, Peterson SS, 2000. Management of *Osmia lignaria* (Hymenoptera: Megachilidae) populations for almond pollination: methods to advance bee emergence. *Environmental Entomology*, 29(5): 874–883.
- Bosch J, Kemp WP, 2001. How to manage the blue orchard bee, *Osmia lignaria*, as an orchard pollinator. Sustainable Agriculture Network, Washington DC.
- Bosch J, Kemp WP, 2002. Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *Bulletin of Entomological Research*, 92(1): 3–16.
- Bosch J, Kemp WP, 2003. Effect of wintering duration and temperature on survival and emergence time in males of the orchard polli-nator *Osmia lingaria* (Hymenoptera: Megachilidae). *Environmental Entomology*, 32(4): 711–716.
- Bosch J, Kemp WP, 2004. Effect of pre-wintering and wintering temperature regimes on weight loss, survival, and emergence time in the mason bee *Osmia cornuta* (Hymenoptera: Megachilidae). *Apidologie*, 35(5): 469–479.
- Bosch J, Vicens N, 2006. Relationship between body size, provisioning rate, longevity and reproductive success in females of the solitary bee *Osmia cornuta*. *Behavioral Ecology and Sociobiology*, 60(1): 26–33.
- Brittain C, Williams N, Kremen C, Klein AM, 2013. Synergistic effects of non-Apis bees and honey bees for pollination services. *Proceedings of the Royal Society of London B: Biological Sciences*, 280(1754): 1–7.
- Cao YB, Zhou XH, Ye BH, Li LL, Lu ZB, Xu H, Li WQ, Yu Y, Men XY, 2017. Restriction factors to *Osmia excavata* Alfken populations in apple orchards of Shandong Province. *Chinese Journal of Applied Entomology*, 54(4): 652–659. [曹衍斌, 周仙红, 叶保华, 李丽莉, 卢增斌, 徐衡, 李文强, 于毅, 门兴元, 2017. 山东苹果园凹唇壁蜂种群的制约因子分析. 应用昆虫学报, 54(4):652–659.]
- Conrad T, Ayasse M, 2015. The role of vibrations in population divergence in the red mason bee, *Osmia bicornis*. *Current Biology*, 25(21): 2819–2822.
- Conrad T, Paxton RJ, Barth FG, Wittko F, Ayasse M, 2010. Female choice in the red mason bee, *Osmia rufa* (L.) (Megachilidae). *The Journal of Experimental Biology*, 213(23): 4065–4073.
- Corliss J, 1992. What's a better blueberry pollinator? *Agricultural Research*, 40(3): 19.
- Ding N, Xin XG, Zhou XH, Men XY, Yu Y, Zhang AS, Li LL, Zhuang QY, 2013. Effects of body weight and feeding on the flight capacity of adults of *Osmia excavata* (Hymenoptera: Megachilidae). *Acta Entomologica Sinica*, 56(8): 884–889. [丁

- 楠, 辛星光, 周仙红, 门兴元, 于毅, 张安盛, 李丽莉, 庄乾营, 2013. 凹唇壁蜂成蜂体重与取食对其飞行能力的影响. 昆虫学报, 56(8): 884–889.]
- Dmochowska K, Giejdasz K, Fliszkiewicz M, Żółtowska K, 2013. Prolonged postdiapause: Influence on some indicators of carbohydrate and lipid metabolism of the red mason bee, *Osmia rufa*. *Journal of Insect Science*, 13:77. Available online: <http://www.insectscience.org/13.77>.
- Dmochowska K, Giejdasz K, Fliszkiewicz M, Żółtowska K, 2012. Changes in the antioxidative system of the red mason bee (*Osmia rufa*) (Hymenoptera: Megachilidae) induced by artificially elongated diapause. *Journal of Apicultural Science*, 56(1): 99–106.
- Elias J, Dorn S, Mazzi D, 2010. Inbreeding in a natural population of the gregarious parasitoid wasp *Cotesia glomerata*. *Molecular Ecology*, 19(11): 2336–2345.
- Fründ J, Zieger SL, Tschamtk T, 2013. Response diversity of wild bees to overwintering temperatures. *Oecologia*, 173(4): 1639–1648.
- 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, Dudenhöffer JH, Freitas BM, Ghazoul J, Greenleaf S, Hipólito J, Holzschuh A, Howlett B, Isaacs R, Javorek S, 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, Rundlöf M, Seymour CL, Schüepp C, Szentgyörgyi H, Taki H, Tschamtk T, Vergara C, 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.
- Gathmann A, Tschamtk T, 2002. Foraging ranges of solitary bees. *Journal of Animal Ecology*, 71 (5): 757–764.
- Gong SX, Zhao GH, Zhao XQ, Li XY, Shi AX, Yang YJ, Nuo AD, 2008. Application of *Osmia excavata* (Alfken) pollination technique for apple production in Yunnan Altiplano. Proceedings of the Entomological Society Annual Conference 2009. Yunnan province. 213–216. [龚声信, 赵高慧, 赵雪晴, 李向永, 石安宪, 杨毅娟, 诺爱东, 2008. 凹唇壁蜂授粉对苹果果形质量的影响. 云南省昆虫学会 2009 年年会论文集. 213–216.]
- Gruber B, Eckel K, Everaars J, Dormann CF, 2011. On managing the red mason bee (*Osmia bicornis*) in apple orchards. *Apidologie*, 42(5): 564–576.
- Haider M, Dorn S, Müller A, 2013. Intra- and interpopulational variation in the ability of a solitary bee species to develop on non-host pollen: implications for host range expansion. *Functional Ecology*, 27(1): 255–263.
- Heimbach F, Russ A, Schimmer M, Born K, 2016. Large-scale monitoring of effects of clothianidin dressed oilseed rape seeds on pollinating insects in Northern Germany: implementation of the monitoring project and its representativeness. *Ecotoxicology*, 25(9): 1630–1647.
- He WZ, Zhou WR, 2009. *Osmia excavata* alfken, *Apis mellifera* and study on the effect of artificial pollination on apple pollination. *Apiculture of China*, 60(11): 9–11, 15. [何伟志, 周伟儒, 2009. 凹唇壁蜂、意大利蜜蜂与人工授粉对苹果授粉效果研究. 中国蜂业, 60(11): 9–11, 15.]
- Holm SN, 1974. *Osmia rufa* (Hymenoptera: Megachilidae) as a pollinator of plants in greenhouses. *Insect Systematics & Evolution*, 4(3): 217–224.
- Holzschuh A, Dudenhöffer JH, Tschamtk T, 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biological Conservation*, 153: 101–107.
- Ingolf S, Susanne S, 2004. Nest-site fidelity, body weight and population size of the red mason bee, *Osmia rufa* (Hymenoptera: Megachilidae), evaluated by mark-recapture experiments. *Entomologia Generalis*, 27 (2): 123–131.
- Jauker F, Petera F, Wolters V, Diekötter T, 2012. Early reproductive benefits of mass-flowering crops to the solitary bee *Osmia rufa* outbalance post-flowering disadvantages. *Basic and Applied Ecology*, 13(3): 268–276.
- Jin DY, Lv SL, 2007. The activity of wild and orchard *Osmia cornifrons*. *Chinese Bulletin of Entomology*, 44(2): 275–276. [金大勇, 吕石龙, 2007. 野生角额壁蜂与果园角额壁蜂的生活力. 昆虫知识, 44(2): 275–276.]
- Karsten S, Karin U, Norbert M, 2010. Conditional sex allocation in the Red Mason bee, *Osmia rufa*. *Behavioral Ecology and Sociobiology*, 64 (3): 337–347.
- Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tschamtk T, 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B*, 274(1608): 303–313.
- Krunic M, Stanisavljevic L, 2006a. Augmentation of managed populations of *Osmia cornuta* and *O. rufa* (Hymenoptera: Megachilidae) in Southeastern Europe. *European Journal of Entomology*, 103(3): 695–697.
- Krunic MD, Stanisavljevic LZ, 2006b. Super-cooling points and diapauses termination in overwintering adults of orchard bees *Osmia cornuta* and *O. rufa* (Hymenoptera: Megachilidae). *Bulletin of Entomological Research*, 96(3): 323–326.
- Liu L, Li LL, Li C, Yuan R, Yu Y, Men XY, Ye BH, 2018. Population investigation and restriction factors to *Osmia excavata* Alfken

- populations of the Shandong Peninsula in 2017. *Apiculture of China*, 69(7): 68–71. [刘丽, 李丽莉, 李超, 袁锐, 于毅, 门兴元, 叶保华, 2018. 胶东地区凹唇壁蜂种群调查及限制因子分析. *中国蜂业*, 69(7): 68–71.]
- Liu XS, Wei SG, 1997. The effect of pollination studies in cherry orchard with the release of *Osmia excavata* (Alfken). *Journal of Hebei Agrotechnical Teachers College*, 11(4): 21–25. [刘新生, 魏枢阁, 1997. 樱桃园凹唇壁蜂释放及授粉效果的研究. *河北农业技术师范学院学报*, 11(4): 21–25.]
- Lundin O, Rundlöf M, Smith HG, Fries I, Bommarco R, 2015. Neonicotinoid insecticides and their impacts on bees: A systematic review of research approaches and identification of knowledge gaps. *PLoS ONE*, 10: e0136928
- Lv JM, Lu LN, Liu ZT, Wang FH, Hou BM, Wang JY, 1993. A new breed of bee that pollinates apples “*Osmia excavata* Alfken”. *China Fruits*, (1): 29–30. [吕家睦, 路灵南, 刘作亭, 王凤华, 侯宝, 王金玉, 1993. 苹果传粉的新蜂种 “凹唇壁蜂”. *中国果树*, (1): 29–30.]
- Lv JM, Lu LN, Liu ZT, 1992. Pollination experiment of apple trees using local wild bee-*Osmia excavata* Atik. *China Fruits*, (1): 29–30. [吕家睦, 路灵南, 刘作亭, 1992. 苹果利用当地野生蜂-凹唇壁蜂传粉试验. *落叶果树*, (1): 14–15.]
- Maeta Y, Kitamura T, 1981. Pollinating efficiency by *Osmia cornifrons* (Radoszkowski) in relation to required number of nesting bees for economic fruit production. *Honeybee Science*, 2(1): 65–72.
- Maini S, Medrzycki P, Porrini C, 2010. The puzzle of honey bee losses: a brief review. *Bull. Insectology*, 63(1): 153–160.
- Matsumoto S, Maejima T, 2010. Several new aspects of the foraging behavior of *Osmia cornifrons* in an apple orchard. Article ID 384371.
- McKinney MI, Park YL, 2012. Nesting activity and behavior of *Osmia cornifrons* (Hymenoptera: Megachilidae) elucidated using videography. *Psyche*, doi: 10.1155/2012/814097.
- Menzel R, Steinmann E, De Souza J, Backhaus W, 1988. Spectral sensitivity of photoreceptors and colour vision in the solitary bee *Osmia rufa*. *Journal of Experimental Biology*, 136(1): 35–52.
- Monzon VH, Bosch J, Retana J, 2004. Foraging behavior and pollinating effectiveness of *Osmia cornuta* (Hymenoptera: Megachilidae) and *Apis mellifera* (Hymenoptera: Apidae) on “Comice” pear. *Apidologie*, 35(6): 575–585.
- Ollerton J, Winfree R, Tarrant S, 2011. How many flowering plants are pollinated by animals? *Oikos*, 120(3): 321–326.
- Phillips JK, Klostermeyer E C, 1978. Nesting behavior of *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society*, (51): 91–108.
- Pisa LW, Amaral-Rogers V, Belzunces LP, Bonmatin JM, Downs CA, Goulson D, Kreutzweiser DP, Krupke C, Liess M, McField M, Morrissey CA, Noome DA, Settele J, Simon-Delso N, Stark JD, Van der Sluijs JP, Van Dyck H, Wiemers M, 2015. Effects of neonicotinoids and fipronil on non-target invertebrates. *Environmental Science and Pollution Research*, 22(1): 68–102.
- Pitts-Singer TL, 2007. Olfactory response of megachilid bees, *Osmia lignaria*, *Megachile rotundata* and *M. pugnata*, to individual cues from old nest cavities. *Environmental Entomology*, 36(2): 402–408.
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE, 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25(6): 345–353.
- Radmacher S, Strohm E, 2010. Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). *Apidologie*, 41 (2): 169–177.
- Radmacher S, Strohm E, 2011. Effects of constant and fluctuating temperatures on the development of the solitary bee *Osmia bicornis* (Hymenoptera: Megachilidae). *Apidologie*, 42(6): 711–720.
- Raw A, 1972. The biology of the solitary bee *Osmia rufa* (L.) (Megachilidae). *Transactions of the Royal Entomological Society of London*, 124(3): 213–229.
- Raw A, O'Toole C, 1979. Errors in the sex of eggs laid by the solitary bee *Osmia rufa* (Megachilidae). *Behaviour*, 70(1): 168–171.
- Rust RW, Torchio PF, 1991. Induction of *Ascosphaera* (Ascomycetes, Ascosphaerales) infections in field populations of *Osmia lignaria propinqua* Cresson (Hymenoptera, Megachilidae). *The Pan-Pacific Entomologist*, 67(4): 251–257.
- Sampson BJ, Cane JH, 2000. Pollination efficiencies of three bee (Hymenoptera: Apoidea) species visiting rabbiteye blueberry. *Journal of Economic Entomology*, 93(6): 1726–1731.
- Sampson BJ, Stringer SJ, Cane JH, Spiers JM, 2004. Screenhouse evaluations of a mason bee *Osmia ribifloris* (Hymenoptera: Megachilidae) as a pollinator for blueberries in the southeastern United States. *Small Fruits Review*, 3(3/4): 381–392.
- Sedivy C, Dorn S, 2014. Towards a sustainable management of bees of the subgenus *Osmia* (Megachilidae; Osmia) as fruit tree pollinators. *Apidologie*, 45(1): 88–105.
- Sedivy C, Muller, A, Dorn S, 2011. Closely related pollen generalist bees differ in their ability to develop on the same pollen diet: evidence for physiological adaptations to digest pollen. *Functional Ecology*, 25(3): 718–725.
- Siedelmann K. 1999. The race for females: The mating system of the

- red mason bee, *Osmia rufa* (L.) (Hymenoptera: Megachilidae). *Journal of Insect Behavior*, 12 (1): 13–25.
- Seidelmann K, 2015. Double insurance of paternity by a novel type of mating plug in a monandrous solitary mason bee *Osmia bicornis* (Hymenoptera: Megachilidae). *Biological Journal of the Linnean Society*, 115(1): 28–37.
- Seidelmann K, Ulbrich K, Mielenz N, 2010. Conditional sex allocation in the red mason bee, *Osmia rufa*. *Biological Journal of the Linnean Society*, 64(3): 337–347.
- Sgolastra F, Medrzycki P, Bortolotti L, Renzi MT, Tosi S, Bogo G, Teper D, Porrini C, Molowny-Horas R, Bosch, J, 2016. Synergistic mortality between a neonicotinoid insecticide and an ergosterol-biosynthesis-inhibiting fungicide in three bee species. *Pest Management Science*. doi: 10.1002/ps.4449.
- Sgolastra F, Kemp WP, Buckner JS, Pitts-Singer TL, Maini S, Bosch J, 2011. The long summer: pre-wintering temperatures affect metabolic expenditure and winter survival in a solitary bee. *Journal of Insect Physiology*, 57(12): 1651–1659.
- Sgolastra F, Kemp WP, Maini S, Bosch J, 2012. Duration of prepupal summer dormancy regulates synchronization of adult diapause with winter temperatures in bees of the genus *Osmia*. *Journal of Insect Physiology*, 58(7): 924–933.
- Sedivy C, Dorn D, 2014. Towards a sustainable management of bees of the subgenus *Osmia* (Megachilidae; *Osmia*) as fruit tree pollinators. *Apidologie*, 45(1): 88–105.
- Sun JS, Wang HY, Lei HD, Zhang Y, Jin HJ, 1999. Bee pollination effects on fruit setting and quality of Red Fuji apple. *Hebei Journal of Forestry and Orchard Research*, 14(4): 316–319. [孙建设, 王海英, 雷宏典, 张英, 靳海军, 1999. 壁蜂传粉对红富士苹果坐果及品质的影响. 河北林果研究, 14(4): 316–319.]
- Tepedino VJ, Torchio PF, 1982. Temporal variability in the sex-ratio of a nonsocial bee, *Osmia lignaria* propinqua-extrinsic determination or the tracking of an optimum. *Oikos*, 38(2): 177–182.
- Teper D, Biliński M, 2009. Red mason bee (*Osmia rufa* L.) as a pollinator of rape plantations. *Journal of Apicultural Science*, 53(2): 115–120.
- Torchio PF, 1976. Use of *Osmia lignaria* (Hymenoptera: Apoidea: Megachilidae) as a pollinator in an apple and prune orchard. *Journal of the Kansas Entomological Society*, 49(4): 475–482.
- Torchio PF, 1981. Field experiments with *Osmia lignaria propinqua* Cresson as a pollinator in almond orchards 1. 1975 studies (Hymenoptera, Megachilidae). *Journal of the Kansas Entomological Society*, 54(4): 815–823.
- Torchio PF, 1985. Field experiments with the pollinator species, *Osmia lignaria propinqua* Cresson, in apple orchards 5. (1979–1980), methods of introducing bees, nesting success, seed counts, fruit yields (Hymenoptera, Megachilidae). *Journal of the Kansas Entomological Society*, 58(3): 448–464.
- Torchio PF, 1987. Use of non-honey bee species as pollinators of crops. *Proceedings of the Entomological Society of Ontario*, 13(2): 102–105.
- Torchio PF, Asensio E, Thorp RW, 1987. Introduction of the European bee, *Osmia cornuta*, into California almond orchards (Hymenoptera, Megachilidae). *Environmental Entomology*, 16(3): 664–667.
- Torchio PF, 1990. *Osmia ribifloris*, a native bee species developed as a commercially managed pollinator of highbush blueberry (Hymenoptera, Megachilidae). *Journal of the Kansas Entomological Society*, 63(3): 427–436.
- Vicens N, Bosch J, 2000. Pollinating efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on ‘red Delicious’ apple. *Environmental Entomology*, 29(2): 235–240.
- Wang FH, Yang F, 2007. Testing of *Osmia excavata* (Alfken) pollination in orchards application. *China Fruits*, (6): 41–43. [王凤鹤, 杨甫, 2007. 凹唇壁蜂果园授粉应用技术试验. 中国果树, (6): 41–43.]
- Wang GP, Cha YL, Ma M, Liu C, Wang JZ, 2013. Research on *Osmia* biology and the result of pollination of apple by *Osmia* bees in the different apple production area. *Chinese Agricultural Science Bulletin*, (34): 171–176. [王贵平, 查养良, 马明, 刘畅, 王金政, 2013. 不同苹果产区壁蜂授粉生物学特性及授粉效应研究. 中国农学通报, (34): 171–176.]
- Wasielewski O, Wojciechowicz T, Giejdasz K, Krishnan N, 2011. Influence of methoprene and temperature on diapause termination in adult females of the over-wintering solitary bee, *Osmia rufa* L. *Journal of Insect Physiology*, 52 (12): 1682–1688.
- Wasielewski O, Wojciechowicz T, Giejdasz K, Krishnan N, 2013. Overwintering strategies in the red mason solitary bee-physiological correlates of midgut metabolic activity and turnover of nutrient reserves in females of *Osmia bicornis*. *Apidologie*, 44(6): 642–656.
- Wei SG, Wang R, Smirle MJ, Xu HL, 2002. Release of *Osmia excavata* and *Osmia jacoti* (Hymenoptera: Megachilidae) for apple pollination. *The Canadian Entomologist*, 134(3): 369–380.
- Wei SG, Wang R, 1990. Raising the amount apple fruit set and production utilizing the domesticated *Osmia cornifrons*. *China Fruits*, (1): 31–32. [魏枢阁, 王韧, 1990. 利用驯化的角额壁蜂提高苹果树座果率及产量. 中国果树, (1): 31–32.]
- Wei SW, Wang Y, Wang HW, 2012. Preliminary report on the effect

- of bee pollination and artificial pollination on fruit set of dangshan crisp pear deciduous fruits. *Deciduous Fruits*, 44(3): 5–6. [魏树伟, 王越, 王宏伟, 2012. 壁蜂授粉加人工授粉对砀山酥梨坐果率的影响研究初报. *落叶果树*, 44(3): 5–6.]
- Wei YP, Yuan F, Zhang YL, 2001. The resistant and reproductive potential of *Osmia excavata* Alfken. *Entomological Knowledge*, 38(2): 122–124. [魏永平, 袁锋, 张雅林, 2001. 凹唇壁蜂的耐寒性及生殖潜力研究. *昆虫知识*, 38(2): 122–124.]
- Wei YP, Yuan F, Zhang YL, 2000. Flower-visiting habits of *Osmia excavata* alfken and the necessary amount of honey bees. *Journal of Northwest A & F University*, 28(5): 76–79. [魏永平, 袁锋, 张雅林, 2000. 凹唇壁蜂的访花习性及其必要放蜂量. *西北农业大学学报*, 28(5): 76–79.]
- White J, Son Y, Park YL, 2009. Temperature-dependent emergence of *Osmia cornifrons* (Hymenoptera: Megachilidae) adults. *Journal of Economic Entomology*, 102(6): 2026–2032.
- Winfree R, 2010. The conservation and restoration of wild bees. *Annals of the New York Academy of Sciences*, 1195(1): 169–197.
- Wu CC, Li PB, Cao ML, Liu HM, Cao CR, Yang LL, 2016. Comparaative study of wall bees and honeybee pollination characteristics in cotton cytoplasmic male sterile lines. *Cotton Science*, 28(4): 369–374. [吴翠翠, 李朋波, 曹美莲, 刘惠民, 曹彩荣, 杨六六, 2016. 壁蜂与蜜蜂对棉花胞质雄性不育系的传粉特性比较. *棉花学报*, 28(4): 369–374.]
- Yamada M, 1990. Control of the chaetodactylus mite, *Chaetodactylus nipponicus* Kurosa, an important mortality agent of hornfaced osmia bee, *Osmia cornifrons* Radoszkowski. Bulletin of the Aomori Apple Experiment Station. 39–77.
- Yang LL, Wu YR, Zhou WR. 1997a. Niche comparative study of apple orchards *Osmia excavate* Atik and *O. jacoti* Cockerell. *Acta Entomologica Sinica*, 40(3): 265–270. [杨龙龙, 吴燕如, 周伟儒, 1997a. 苹果园中凹唇壁蜂和紫壁蜂的生态位比较研究. *昆虫学报*, 40(3): 265–270.]
- Yang LL, Xu HL, Wu YR, 1997b. Comparative studies of nesting and foraging behavior and pollination ecology of *Osmia excavata* Alfken and *O. jacoti* Cockerell in apple orchards (Hymenoptera: Megachilidae). *Acta Ecologica*, 17(1): 1–6. [杨龙龙, 徐环李, 吴燕如, 1997b. 凹唇壁蜂和紫壁蜂筑巢、访花行为和传粉生态学的比较研究. *生态学报*, 17(1): 1–6.]
- Yuan R, Li LL, Li C, Xia XJ, Zheng L, Yu Y, Men XY, 2018. Toxicity and hazard assessment of six neonicotinoid insecticides on *Osmia excavata* (Hymenoptera: Megachilidae). *Acta Entomologica Sinica*, 61(8): 950–956. [袁锐, 李丽莉, 李超, 夏小菊, 郑礼, 于毅, 门兴元, 2018. 六种新烟碱类杀虫剂对凹唇壁蜂的毒性及风险评估. *昆虫学报*, 61(8): 950–956.]
- Zhang CX, Tang XD, Cheng JA, 2008. The utilization and industrialization of insect resources in China. *Entomological Research*, 38(S1): 38–47.
- Zhai H, Wang GP, Xue XM, 2015. Preliminary investigation of mite damage to pollinate *Osmia* nest in apple producing areas in Shandong province. *China Fruit*, (6): 82–84. [翟浩, 王贵平, 薛晓敏, 2015. 山东省主要苹果产区授粉壁蜂巢螨害情况调查初报. *中国果树*, (6): 82–84.]
- Zhou XH, Song MJ, Cao YB, Zhang AS, Li LL, Men XY, Zhang SC, Zhuang QY, Zhai YF, Yu Y, 2017. Screen safe chemicals for *Osmia excavata* Alfken against the parasitic mite (*Tortonia* sp.) in the laboratory. *Journal of Environmental Entomology*, 39(2): 411–418. [周仙红, 宋美佳, 曹衍斌, 张安盛, 李丽莉, 门兴元, 张思聪, 庄乾营, 翟一凡, 于毅, 2017. 凹唇壁蜂寄生螨安全防治药剂的筛选. *环境昆虫学*, 39(2): 411–418.]
- Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S, 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, 143(3): 669–676.