

熊蜂主要病虫害的发生和危害现状*

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摘 要 熊蜂以其独有的形态特征与生物学特性, 在植物授粉中发挥着十分重要作用。然而受寄生虫、真菌等多种病原体影响, 近几十年来全球多个地区熊蜂多样性急剧下降。欧洲地熊蜂 *Bombus terrestris* 在全球商业化推广应用, 加剧了相关熊蜂病虫害的传播和蔓延, 已在多地造成生物入侵危害, 导致当地传粉蜂多样性下降。本文综述了熊蜂主要病虫害的种类、危害和传播情况, 以期有全面深入的认识, 并提出对进口商业化熊蜂的管理措施, 为我国本土熊蜂资源保护研究奠定基础。

关键词 熊蜂; 病虫害; 危害; 保护措施

Occurrence and current status of the main pathogens and parasites of bumblebees

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Abstract Due to their unique morphological characteristics and bionomics bumblebees play an important role in plant pollination. However, various pathogens such as parasites and fungi, have caused the diversity of bumblebees to decline sharply in many parts of the world in recent decades. The global commercial supply and application of the European bumblebee, *Bombus terrestris*, has intensified the spread of bumblebee pathogens and has led to this species becoming invasive in many places, resulting in a decline in local bee pollinators. This article reviews the types, hazards, and spread of the main bumblebee pathogens and parasites, and proposes management measures for imported commercial bumblebees, thereby laying a foundation for the protection of native Chinese bumblebees.

Key words bumblebees; pests; harms; protective measures

熊蜂隶属膜翅目 Hymenoptera、蜜蜂科 Apidae、熊蜂属 *Bombus*, 其体型粗大、密被绒毛、吻长、访花时声震行为明显, 是众多野生植物和农作物的重要传粉昆虫。同时, 和家养蜜蜂相比, 熊蜂进化程度低, 对低温、低光照环境适应性强, 适合为温室作物传粉, 尤其为茄科作物传粉效果十分显著(安建东等, 1999)。熊蜂传粉在促进坐果、提高产量、改善品质、节约劳动力、减少激素及农药残留方面优势明显(安建东等, 2004)。每年, 番茄等作物因熊蜂传粉而产

生的经济价值高达数百亿美元(Velthuis and van Doorn, 2006), 熊蜂传粉在设施农业生产中发挥着巨大作用。

虽然熊蜂具有重要的生态及经济价值, 但全球范围内熊蜂的种类以及分布范围正不断下降。目前, 已被评估的 150 种熊蜂, 有 36 种(24%)被列入国际自然保护联盟濒危物种红色名录(Cameron and Sadd, 2020)。病虫害威胁是导致熊蜂多样性下降的重要因素之一(Otterstatter and Thomson, 2008; Schmid-Hempel *et al.*,

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2014)。本文对熊蜂携带病虫害的种类、主要危害以及传播情况进行总结,并提出相应的预防策略,旨在为商业化熊蜂的科学使用和本土熊蜂资源保护提供参考。

1 主要寄生虫

1.1 熊蜂孢子虫

1.1.1 主要危害 熊蜂孢子虫 *Apicystis bombi* 属于新簇虫目 Neogregarinorida, 主要寄生在熊蜂脂肪体中, 也可在蜂巢的花粉及粪便中存活, 通过粪口传播方式感染其它熊蜂个体 (Lipa and Triggiani, 1996; Graystock *et al.*, 2013)。熊蜂孢子虫危害较大, 可降低蜂王滞育后的存活率、缩短工蜂寿命、增加工蜂死亡率 (Rutrecht and Brown, 2008; Graystock *et al.*, 2016)。脂肪体是熊蜂有关免疫和新陈代谢的生化反应的重要场所 (Arrese and Soulages, 2010), 感染熊蜂孢子虫之后, 熊蜂体内脂肪明显减少, 脂肪/脂质含量可下降 17%, 从而对其生理及行为造成严重影响 (Graystock *et al.*, 2016)。

1.1.2 传播情况 熊蜂孢子虫最初在加拿大的熊蜂中被检测到并被命名为 *Mattesia bombi* (Liu *et al.*, 1974), 1996 年被重新命名为 *Apicystis bombi* (Lipa and Triggiani, 1996)。20 世纪 80-90 年代, 在加拿大、芬兰、法国、意大利和瑞士等国的熊蜂中陆续检测到熊蜂孢子虫 (Lipa and Triggiani, 1996), 近年来在北美、南美和亚洲等地区, 也检测到熊蜂与蜜蜂被该寄生虫感染 (Colla *et al.*, 2006; Plischuk and Lange, 2009; Plischuk *et al.*, 2011; Morimoto *et al.*, 2013)。熊蜂孢子虫可随着商业化熊蜂的流通进行跨种群、跨地域传播。在墨西哥和英国使用的商业化蜂群中, 熊蜂孢子虫的感染率均较高 (Graystock *et al.*, 2013; Sachman-Ruiz *et al.*, 2015); 在土耳其, 野外收集的 578 只地熊蜂 *Bombus terrestris* 蜂王的感染率为 8.54% (Cankaya and Osman, 2006); 入侵阿根廷巴塔哥尼亚地区的地熊蜂, 感染熊蜂孢子虫的比例为 12.1% (Plischuk *et al.*, 2011)。

1.2 熊蜂短膜虫

1.2.1 主要危害 熊蜂短膜虫 *Crithidia bombi* 属于动质目 Kinetoplastida 锥虫科 Trypanosomatidae 短膜虫属 *Crithidia*, 是一种寄生在熊蜂肠道内带有鞭毛的锥虫, 附着于寄主肠壁上进行繁殖 (Schmid-Hempel, 2001)。熊蜂短膜虫随寄主粪便排出体外, 可污染蜂巢和野外开花植物, 健康蜂在接触到这些污染物时可能会被侵染, 从而使其传播扩散 (Schmid-Hempel and Schmid-Hempel, 1993; Durrer and Schmid-Hempel, 1994)。被熊蜂短膜虫感染后, 地熊蜂蜂王繁殖后代的成群率以及子代工蜂、雄性蜂和蜂王的数量都明显下降 (Brown *et al.*, 2003); 熊蜂短膜虫还能损伤工蜂的认知能力, 从而影响其采集行为 (Gegear *et al.*, 2005, 2006)。通常情况下, 熊蜂短膜虫对寄主的危害较轻, 但如果寄主同时受到其他压力胁迫, 将加剧熊蜂短膜虫的危害程度。研究表明, 感染熊蜂短膜虫的工蜂受到饥饿刺激, 其死亡率会提高 50%, 并且, 染病个体的资源分配模式也会发生变化, 它们会把更多的资源用于脂肪体而非生殖系统的发育 (Brown *et al.*, 2000)。

1.2.2 传播情况 Lipa 和 Triggiani (1988) 在地熊蜂中首次发现了熊蜂短膜虫。随后, 在 *Bombus lapidarius*、早熊蜂 *Bombus pratorum*、明亮熊蜂 *Bombus lucorum*、*Bombus mesomelas*、*Bombus monticola*、*Bombus pyrenaicus*、红柄熊蜂 *Bombus ruderalis*、西氏熊蜂 *Bombus sichelii*、*Bombus wurflenii* 等多种熊蜂中检测到了熊蜂短膜虫 (Korner and Schmid-Hempel, 2005)。近年来在地熊蜂、长颊熊蜂 *Bombus hortorum*、牧场熊蜂 *Bombus pascuorum*、*Bombus lapidarius* 等蜂种中也检测到了熊蜂短膜虫 (Erler *et al.*, 2012; Goulson *et al.*, 2017)。不同地区、不同蜂种及不同级型的熊蜂感染熊蜂短膜虫的比例有所差异。在西班牙, 地熊蜂检出熊蜂短膜虫的平均感染率为 15.7% (Jabal-Uriel *et al.*, 2017)。唐裕杰等 (2019) 检测了中国内蒙古、甘肃、青海和四川 4 省区的 25 种熊蜂, 发现熊蜂短膜虫的平均感染率为 26.0%, 4 个地区中青海熊蜂的感染率

最高 (48.2%); 25 种熊蜂中白背熊蜂 *Bombus festivus* 和火红熊蜂 *Bombus pyrosoma* 的感染率明显高于其它蜂种, 分别为 70% 与 66.7%。与工蜂和蜂王相比, 雄性蜂感染熊蜂短膜虫的比例较高 (Jabal-Uriel *et al.*, 2017; 唐裕杰等, 2019), 这可能是由于成年雄性蜂主要生活在蜂巢外的环境中, 更易受到其它染病蜂的传染 (Goulson, 2010)。

1.3 布赫纳蝗螨

1.3.1 主要危害 布赫纳蝗螨 *Locustacarus buchneri* 属于恙螨目 Trombidiformes 蝗螨科 Podapolipidae 蝗螨属 *Locustacarus*, 是一种内部寄生螨, 主要寄生在熊蜂腹部的气囊中 (Yoneda *et al.*, 2008)。成年雌螨可吸食熊蜂气管内的血淋巴, 大量布赫纳蝗螨在工蜂体内累积, 可造成寄主腹泻和访花活动减少 (Husband and Sinha, 1970)。感染布赫纳蝗螨会缩短工蜂及雄性蜂的寿命、减缓蜂群的发展速度 (Otterstatter and Whidden, 2004)、改变工蜂的访花行为 (Otterstatter *et al.*, 2005), 从而影响传粉效率。

1.3.2 传播情况 布赫纳蝗螨分布较广, 目前已在近 30 种熊蜂中被检测到。野外熊蜂的感染率通常低于 10% (Macfarlane *et al.*, 1995), 但感染率受季节、蜂种、工蜂蜂王等级型的影响 (Otterstatter and Whidden, 2004)。加拿大亚伯达地区野生熊蜂种群的平均感染率为 7.9%; 土耳其越冬后的地熊蜂蜂王的平均感染率为 5.28% (Cankaya and Osman, 2006); 1998-1999 年日本引进商业化地熊蜂的平均感染率为 20% (Goka *et al.*, 2000), 明显高于日本本土熊蜂 0-8% 的感染率 (Goka *et al.*, 2001); 在智利, 入侵种地熊蜂的感染率 (41%) 亦明显高于本土熊蜂 *Bombus rudratus* (31%) 和 *Bombus dahlbomii* (23%) (Arismendi *et al.*, 2016)。

1.4 蜂巢小甲虫

1.4.1 主要危害 蜂巢小甲虫 *Aethina tumida* 属于鞘翅目 Coleoptera 露尾甲科 Nitidulidae, 起源于非洲撒哈拉以南地区。由于西方蜜蜂非洲亚种

具有多种抗性机制, 蜂巢小甲虫在其起源地带来的危害较小。但随着分布区的自然扩展以及受感染蜂群的流动, 蜂巢小甲虫已传播到很多地方, 给西方蜜蜂欧洲亚种的养殖带来巨大损失 (Neumann *et al.*, 2016)。蜂巢小甲虫可取食蜜蜂幼虫、花粉、蜜脾等, 造成蜂蜜发酵、巢脾损毁, 导致蜂王停止产卵和蜂群逃逸 (Amos *et al.*, 2018)。雌性蜂巢小甲虫还可在蜜蜂巢房蜡盖上咬洞, 在蜜蜂蛹或预蛹上产卵 (Ellis *et al.*, 2004), 可明显影响子脾面积、蜂群群势以及蜜蜂的飞行能力 (Ellis *et al.*, 2003), 2 周时间内即可摧毁整群蜜蜂 (Neumann *et al.*, 2010)。室内研究表明, 蜂巢小甲虫可在燥熊蜂 *Bombus impatiens* 中繁殖并影响其蜂群发展, 被蜂巢小甲虫寄生后, 熊蜂死亡率和蜂巢破坏度增加, 蜂群变小 (Ambrose *et al.*, 2000; Stanghellini *et al.*, 2000)。蜂巢小甲虫还可能作为载体传播多种病原体 (de Landa *et al.*, 2020)。

1.4.2 传播情况 1996 年蜂巢小甲虫首次在美国发现, 之后其分布地区陆续扩展到埃及 (2000 年)、澳大利亚 (2001 年)、加拿大 (2002 年)、葡萄牙 (2004 年)、牙买加 (2005 年)、墨西哥 (2007 年)、意大利 (2014 年) 及菲律宾 (2014 年) 等地 (Neumann *et al.*, 2016)。目前, 蜂巢小甲虫已传播至墨西哥的 14 个州 (de Landa *et al.*, 2020) 及美国的 48 个州, 对夏威夷、佛罗里达及美国东南部的养蜂业造成了严重危害, 是蜂群消失的主要原因; 在加拿大已数次暴发 (Neumann *et al.*, 2016)。2014 年 6 月, 蜂巢小甲虫在亚洲菲律宾首次暴发, 截至 2015 年 4 月即造成棉兰老岛数百群西方蜜蜂被毁 (Chantawannakul *et al.*, 2016)。2017 年, 我国广东省汕尾新国镇首次发现蜂巢小甲虫, 它对当地东方蜜蜂 *Apis cerana* 和西方蜜蜂 *Apis mellifera* 均造成严重危害 (赵红霞等, 2018); 2018 年在海南省亦有该虫的危害报告 (赵红霞等, 2019)。此外, 熊蜂和无刺蜂等野生蜂也是蜂巢小甲虫的潜在寄主 (Stanghellini *et al.*, 2000; Halcroft *et al.*, 2011), 蜂巢小甲虫已成为全球养蜂业以及野生蜜蜂面临的巨大威胁。

2 真菌、病毒、蜜蜂螺原体等其它病原物

2.1 真菌

2.1.1 熊蜂微孢子虫 熊蜂微孢子虫 *Nosema bombi* 属于微孢子虫目 Microsporidia 微孢子科 Nosematidae 微孢子属 *Nosema*, 主要寄生在熊蜂的消化道和马氏管中, 可通过工蜂迷巢、采集污染的植物以及饲喂污染的花粉等途径传播 (Fantham and Porter, 1914; Meeus *et al.*, 2011)。感染熊蜂微孢子虫后, 熊蜂脂肪体减少, 受感染的蜂王卵巢较小 (Fantham and Porter, 1914)、建立蜂群的成功率下降 (van der Steen, 2008), 寄主熊蜂会因腹部肿胀而行动迟缓、失去飞行能力, 从而使采集能力受到严重影响。地熊蜂被熊蜂微孢子虫感染后, 工蜂存活率下降、清理蜂巢能力变弱, 雄性蜂存活率降低、几乎没有精子, 新蜂王腹部肿胀、无法完成交尾飞行 (Otti and Schmid-Hempel, 2007); 熊蜂染病后, 群势较小、不能产生繁殖性后代 (Otti and Schmid-Hempel, 2007, 2008)。

1914 年, Fantham 和 Porter (1914) 首先在地熊蜂等 6 种熊蜂中检测到熊蜂微孢子虫。北美地区, 在快速减少的本土熊蜂物种中检测到较高的感染率, 这可能与引入商业化地熊蜂促进了熊蜂微孢子虫的传播有关 (Cameron *et al.*, 2011)。2011-2013 年在美国堪萨斯州调查的 6 种熊蜂 142 只早春蜂王中, 27% 的 *Bombus pensylvanicus* 蜂王及 13% 的 *Bombus auricomus* 蜂王被熊蜂微孢子虫感染 (Tripodi *et al.*, 2014)。陈文锋等 (2010) 检测了来源于我国甘肃、青海、内蒙古和四川 4 省区的 1 008 只熊蜂, 发现熊蜂微孢子虫总体感染率为 20.8%, 其中白背熊蜂 *Bombus festivus* 和西伯熊蜂 *Bombus sibiricus* 感染率最高, 分别为 75.0% 和 68.6%。众多研究表明, 染病的商业化地熊蜂逃出温室后, 其所携带的熊蜂微孢子虫很可能会传染给附近的野生熊蜂, 从而对当地熊蜂造成威胁 (Colla *et al.*, 2006; Otterstatter and Thomson, 2008)。

2.1.2 白僵菌 白僵菌 *Beauveria bassiana* 属于

肉座菌目 Hypocreales 虫草科 Cordycipitaceae 白僵菌属 *Beauveria*, 为植保工作中普遍使用的昆虫病原真菌, 对蜜蜂相对安全 (Alves *et al.*, 1996)。与蜜蜂相比, 熊蜂调节巢温的能力较弱, 蜂巢内湿度较大、有利于真菌的生长, 特别是早春季节蜂群内工蜂数量较少, 抵抗真菌感染的能力较弱。白僵菌的粉剂对地熊蜂无害, 所以在北美地区该种熊蜂也被用做白僵菌的载体进行防治温室番茄及甜椒等作物的害虫 (Kapongo *et al.*, 2008)。但白僵菌的液体制剂对地熊蜂的触杀毒性明显, 可造成工蜂死亡率升高及雄性蜂数量下降 (Mommaerts *et al.*, 2009)。但 Ramanaidu 和 Cutler (2013) 在评估商品化白僵菌液体制剂对熊蜂的经口毒性和接触毒性时发现, 该制剂对美洲地熊蜂工蜂存活率、工蜂产卵时间以及雄性蜂羽化时间均无明显影响。已有结果之间的差异可能是研究蜂种和毒性评估方法不同造成的。

2.1.3 绿僵菌 绿僵菌 *Metarhizium anisopliae* 属于肉座菌目 Hypocreales 麦角菌科 Clavicipitaceae 绿僵菌属 *Metarhizium*。同白僵菌一样, 绿僵菌也是植物保护工作中较常使用的昆虫病原真菌 (Alves *et al.*, 1996)。Hokkanen 等 (2003) 研究发现, 绿僵菌可以感染明亮熊蜂 *Bombus lucorum*, *Bombus lapidarius* 及地熊蜂, 但其致病性比白僵菌弱。利用地熊蜂作为传播媒介时, 对绿僵菌的使用剂量尚需进一步研究, 以确保媒介昆虫的安全并获得良好的防治效果 (Guy *et al.*, 2013)。

2.2 病毒

蜜蜂病毒多为无症状感染, 但在一定条件下能够迅速复制, 导致明显的症状, 出现翅膀变形、变色、脱毛、腹部肿胀、颤抖、麻痹或死亡 (Chen and Siede, 2007)。目前已鉴定出超过 30 种蜜蜂病毒, 它们多为正义单链 RNA 病毒。其中, 蜜蜂残翅病毒 (Deformed wing virus, DWV)、黑蜂王台病毒 (Black queen cell virus, BQCV)、以色列急性麻痹病毒 (Israeli acute paralysis virus, IAPV)、缓慢性麻痹病毒 (Slow bee paralysis virus, SBPV)、蜜蜂急性麻痹病毒 (Acute bee paralysis virus, ABPV)、囊状幼虫

病毒 (Sacbrood virus, SBV)、卡什米尔病毒 (Kashmir bee virus, KBV)、西奈湖病毒 (Lake Sinai virus, LSV)、蜜蜂慢性麻痹病毒 (Chronic bee paralysis virus, CBPV)、蜜蜂丝状病毒 (*Apis mellifera* filamentous virus, AmFV) 以及类瓦螨病毒 (*Varroa destructor* macula-like virus, VdMLV) 均已在熊蜂中检测到 (Tehel *et al.*, 2016)。部分病毒种类已确定在熊蜂中有致病性, 例如, 多种熊蜂均对 ABPV 比较敏感 (Bailey and Gibbs, 1964); DWV 可造成地熊蜂和牧场熊蜂翅膀畸形, 并且对熊蜂的毒性可能大于蜜蜂 (Genersch *et al.*, 2006); KBV 及 IAPV 均可造成地熊蜂繁殖力下降 (Meeus *et al.*, 2014)。具体病毒类型、被感染熊蜂物种、感染后果、发现

地区和报道文献详见表 1。

2.3 蜜蜂螺原体

蜜蜂螺原体 *Spiroplasma melliferum* 属于虫原体目 Entomoplasmatales 螺原体科 Spiroplasmataceae 螺原体属 *Spiroplasma* (于汉寿等, 2009), 不仅存在于蜜蜂的血淋巴和肠道中, 而且在熊蜂、切叶蜂、食虫虻的血淋巴以及熊蜂和蝴蝶的肠道中都有检出 (Clark *et al.*, 1985; Meeus *et al.*, 2012)。染病蜜蜂排泄在开花植物上的粪便中含有的蜜蜂螺原体可作为污染源感染其他健康个体 (Raju *et al.*, 1981)。蜜蜂螺原体可使受感染蜜蜂产生消化障碍, 造成花粉中毒、寿命缩短 (Clark *et al.*, 1985; Alexeev *et al.*, 2012)。虽然蜜蜂螺原体的

表 1 熊蜂感染蜜蜂病毒的报道
Table 1 Reports on bumblebees infected with bee viruses

蜜蜂病毒 Bee viruses	被感染熊蜂物种 Infected bumblebee species	病毒感染后果 Effects of the virus infection	发现地区 Discovered regions	参考文献 References
蜜蜂残翅病毒 Deformed wing virus	<i>B. atratus</i> <i>B. bimaculatus</i> <i>B. humilis</i> <i>B. impatiens</i> <i>B. lapidarius</i> <i>B. lucorum</i> <i>B. pascuorum</i> <i>B. ternarius</i> <i>B. terrestris</i> <i>B. vagans</i>	翅膀畸形, 褶皱, 死亡率高	南美 北美 欧洲	Genersch <i>et al.</i> , 2006; Meeus <i>et al.</i> , 2010; Singh <i>et al.</i> , 2010; Evison <i>et al.</i> , 2012; Levitt <i>et al.</i> , 2013; Reynaldi <i>et al.</i> , 2013; McMahon <i>et al.</i> , 2015; Gamboa <i>et al.</i> , 2015; Sachman-Ruiz <i>et al.</i> , 2015; Graystock <i>et al.</i> , 2016; Alger <i>et al.</i> , 2019; Toplak <i>et al.</i> , 2020
黑蜂王台病毒 Black queen cell virus	<i>B. atratus</i> <i>B. bimaculatus</i> <i>B. hortorum</i> <i>B. humilis</i> <i>B. huntii</i> <i>B. impatiens</i> <i>B. lapidarius</i> <i>B. lucorum</i> <i>B. pascuorum</i> <i>B. sylvarum</i> <i>B. ternarius</i> <i>B. terrestris</i> <i>B. vagans</i>	无明显症状	南美 北美 欧洲 亚洲	Singh <i>et al.</i> , 2010; Peng <i>et al.</i> , 2011; Levitt <i>et al.</i> , 2013; Reynaldi <i>et al.</i> , 2013; McMahon <i>et al.</i> , 2015; Gamboa <i>et al.</i> , 2015; Choi <i>et al.</i> , 2015; Alger <i>et al.</i> , 2019; Manley <i>et al.</i> , 2020; Toplak <i>et al.</i> , 2020
以色列急性麻痹病毒 Israeli acute paralysis virus	<i>B. impatiens</i> <i>B. ternarius</i> <i>B. vagans</i>	子代产生速度减缓, 雄性蜂产量下降	北美	Singh <i>et al.</i> , 2010; Levitt <i>et al.</i> , 2013; Meeus <i>et al.</i> , 2014; Sachman-Ruiz <i>et al.</i> , 2015

续表 1 (Table 1 continued)

蜜蜂病毒 Bee viruses	被感染熊蜂物种 Infected bumblebee species	病毒感染后果 Effects of the virus infection	发现地区 Discovered regions	参考文献 References
囊状幼虫病毒 Sacbrood virus	<i>B. atratus</i> <i>B. hortorum</i> <i>B. impatiens</i> <i>B. pascuorum</i> <i>B. sylvarum</i> <i>B. ternarius</i> <i>B. terrestris</i> <i>B. vagans</i>	无	南美 北美 欧洲	Singh <i>et al.</i> , 2010; Levitt <i>et al.</i> , 2013; Reynaldi <i>et al.</i> , 2013; McMahon <i>et al.</i> , 2015; Gamboa <i>et al.</i> , 2015; Toplak <i>et al.</i> , 2020
缓慢性麻痹病毒 Slow bee paralysis virus	<i>B. hortorum</i> <i>B. lapidarius</i> <i>B. lucorum</i> <i>B. pascuorum</i> <i>B. terrestris</i>	无	欧洲	McMahon <i>et al.</i> , 2015; Parmentier <i>et al.</i> , 2016; Manley <i>et al.</i> , 2020
蜜蜂急性麻痹病毒 Acute bee paralysis virus	<i>B. atratus</i> <i>B. hortorum</i> <i>B. impatiens</i> <i>B. lapidarius</i> <i>B. lucorum</i> <i>B. pascuorum</i> <i>B. terrestris</i>	瘫痪,进而发展为致命性麻痹症状	南美 北美 欧洲	Bailey <i>et al.</i> , 1964; Meeus <i>et al.</i> , 2010; Gamboa <i>et al.</i> , 2015; McMahon <i>et al.</i> , 2015; Sachman-Ruiz <i>et al.</i> , 2015; Toplak <i>et al.</i> , 2020
卡什米尔病毒 Kashmir bee virus	<i>B. impatiens</i> <i>B. terrestris</i>	启群及子代产生速度减缓,雄性蜂产量下降	北美 欧洲	Meeus <i>et al.</i> , 2010; Meeus <i>et al.</i> , 2014; Sachman-Ruiz <i>et al.</i> , 2015
西奈湖病毒 Lake Sinai virus	<i>B. atratus</i> <i>B. hortorum</i> <i>B. lapidarius</i> <i>B. pascuorum</i> <i>B. sylvarum</i> <i>B. terrestris</i>	无	南美 欧洲	Gamboa <i>et al.</i> , 2015; Parmentier <i>et al.</i> , 2016; Toplak <i>et al.</i> , 2020
蜜蜂慢性麻痹病毒 Chronic bee paralysis virus	<i>B. impatiens</i>	无	北美	Sachman-Ruiz <i>et al.</i> , 2015
蜜蜂丝状病毒 <i>Apis mellifera</i> filamentous virus	<i>B. dahlbomii</i> <i>B. morio</i> <i>B. opifex</i> <i>B. pauloensis</i>	无	南美	Revainera <i>et al.</i> , 2020
类瓦螨病毒 <i>Varroa destructor</i> macula-like virus	<i>B. lapidarius</i> <i>B. pascuorum</i> <i>B. pratorum</i>	无	欧洲	Parmentier <i>et al.</i> , 2016

寄主范围较广,但目前对其致病性的了解十分有限,对熊蜂的具体危害尚未见报道。

3 研究展望

目前,有关熊蜂病虫害的研究主要集中于熊蜂孢子虫、熊蜂短膜虫、布赫纳蝗螨以及熊蜂微孢子虫等。在不同国家和地区、不同蜂种、不同级型感染的病虫害种类及感染程度均有所差异,

不同病虫害造成的危害程度亦不同。但目前的研究多集中在熊蜂的流行病学调查,对相关病虫害的致病机理、不同病虫害的交互作用研究较少。蜜蜂病毒在商业化熊蜂及野生熊蜂中普遍存在,通常认为这些病毒是从蜜蜂中溢出的,但关于它们的传播方向仍需进一步确认 (Singh *et al.*, 2010; Meeus *et al.*, 2011)。病毒的宿主范围较广、可能在广泛的环境中传播,为深入了解它们

对生态系统的影响, 应该在整个膜翅目传粉昆虫群落或更大的类群内分析其流行病学。此外, 随着分子生物学技术的应用, 熊蜂中的许多新病毒也将被揭示 (Pascall *et al.*, 2019)。病原物分子数据的累积、组学技术的发展、熊蜂参考基因组的公布等, 都为深入分析熊蜂病害的致病机理以及传播风险奠定了基础。研究发现, 不同熊蜂物种对病原物的易感性不同、不同病原物之间的互作也有差异, 因此, 进一步分析不同蜂种的抗病机制和免疫防御反应, 可为抗病蜂种的培育奠定基础 (Jabal-Uriel *et al.*, 2017; 唐裕杰等, 2019)。由于很多病害无法凭肉眼鉴别、或无法进行体外培养、或低于检测水平下限, 因此检测结果符合检疫要求的蜂群仍有可能携带病原物。并且, 熊蜂中还有很多新病害尚需鉴定。为降低这种风险, 不仅需要灵敏度高、操作简单的检测技术, 以便在特定水平上快速鉴别出病原物, 更需要在地管理、检验检疫以及后续监管等环节进行严格的风险控制, 特别是在熊蜂饲养过程中, 要尽量消除饲养环境和食物中的病原物, 尽量减少熊蜂病虫害的传播和扩散。

已有大量证据表明, 欧洲地熊蜂等蜂种的商业化贸易加速了相关病原物的传播, 造成多个地区野生熊蜂种群数量下降 (Colla *et al.*, 2006; Arbetman *et al.*, 2013; Schmid-Hempel *et al.*, 2014; Cameron *et al.*, 2016)。外来物种地熊蜂携带的熊蜂孢子虫传播到本土熊蜂中, 可能是造成阿根廷以及南美地区熊蜂减少的主要原因 (Arbetman *et al.*, 2013; Aizen *et al.*, 2018); 商业化地熊蜂感染熊蜂短膜虫 (Plischuk and Lange, 2009; Graystock *et al.*, 2013) 及熊蜂孢子虫 (Cameron *et al.*, 2011) 的比例均较高, 染病的地熊蜂从授粉温室逃逸, 可使附近本土熊蜂的感染率升高 (Colla *et al.*, 2006; Otterstatter and Thomson, 2008); 随着地熊蜂的入侵, 布赫纳蝗螨的欧洲种群已被带入日本, 并感染了当地的熊蜂种群 (Goka *et al.*, 2006)。为尽量避免外来熊蜂病虫害对中国本土传粉昆虫的影响, 我们应该防患于未然, 加强进境熊蜂健康管理, 严防生物入侵; 同时加强对中国境内地熊蜂适生区和易

感种群的监测, 保护本土熊蜂资源 (Naeem, 2018)。在进口熊蜂为我国设施作物传粉时, 建议参考日本等国家的经验, 制定严格的法律法规, 建立完善的监测体系和技术规程, 进行病原物常规筛查, 以便及时发现疫情并妥善处理, 尽量避免引入病原物 (Goka, 2010)。在熊蜂传粉过程中, 温室通风口要设置防虫网防止熊蜂逃逸, 在蜂箱巢门口安装隔王栅防止蜂王外逃定殖; 传粉任务结束后及时销毁蜂巢, 最大限度降低进口熊蜂的不良影响。

20 世纪 70 年代, 熊蜂人工驯养获得成功, 但直到 1987 年才开始商业化生产 (Velthuis and van Doorn, 2006)。目前, 商业化熊蜂的年产量为两百多万群, 其中主要为欧洲地熊蜂 (Graystock *et al.*, 2015)。虽然多个国家已明文禁止进口欧洲地熊蜂, 但目前我国设施农业中应用最多的仍然是荷兰 KOPPERT 公司和比利时 BIOBEST 公司生产的欧洲地熊蜂。最近研究发现, 中国境内有适合欧洲地熊蜂栖息的生境 (Naeem *et al.*, 2018); 一些本土熊蜂还面临地熊蜂造成生殖干扰的威胁 (袁晓龙等, 2018), 表明欧洲地熊蜂入侵中国的风险巨大。全球熊蜂约 260 种 (Cameron and Sadd, 2020), 中国已鉴定出 125 种, 是全球熊蜂物种资源最为丰富的国家 (黄家兴和安建东, 2018)。我国于 1995 年正式立项研究熊蜂利用技术, 近 20 多年来, 先后筛选出了明亮熊蜂 *Bombus lucorum*、密林熊蜂 *Bombus patagiatus*、红光熊蜂 *Bombus ignitus*、火红熊蜂 *Bombus pyrosoma*、重黄熊蜂 *Bombus picipes*、兰州熊蜂 *Bombus lantschouensis*、短头熊蜂 *Bombus breviceps* 和弗里熊蜂 *Bombus friseanus* 等多种可人工驯养的本土蜂种 (梁诗魁等, 1999; 安建东等, 2010; Liang *et al.*, 2020)。但中国本土熊蜂繁育仍处于实验室和中试阶段, 尚不能满足作物规模化授粉需求。为降低外来熊蜂物种入侵的风险, 我国应该进一步加强本土熊蜂人工繁育基础研究, 攻克关键技术难题, 提高繁育效率, 降低生产成本; 同时, 应制定不同地区、不同设施类型、不同作物蜂传粉应用技术规范, 加大科普宣传力度, 推广设施果菜蜂传粉提质增效的技

术模式, 促进设施农业绿色高质量发展。

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