



昆虫迁飞行为及其调控机制*

刘鹏程^{1**} 刁跃珲¹ 郭嘉雯² 高博雅¹ 胡 高^{1***}

(1. 南京农业大学植物保护学院昆虫系, 南京 210095; 2. 浙江省农业科学院植物保护与微生物研究所, 杭州 310021)

摘 要 迁飞是昆虫长期适应资源与环境的季节性变化所形成的一种行为策略。迁飞昆虫不仅通过迁飞逃避不良环境, 也因其极高的繁殖力确保种群在新的生境中实现快速增长甚至暴发成灾, 对整个自然生态系统和农业生态系统影响甚大。本文首先基于部分迁飞概念, 描述了迁飞型和居留型个体在形态、行为、生理上的差异, 重点介绍了迁飞与生殖的耦合关系, 以及诱导迁飞的外界环境因子, 最后综述了昆虫迁飞行为调控的分子机制方面的研究进展。从感受不良环境信号到决定迁飞, 从起飞、飞行、降落到决定继续迁飞或终止迁飞, 这一系列过程受昆虫内分泌、表观等诸多因素的调控, 但其背后的分子机制有待深入研究。

关键词 部分迁飞; 卵子发生与飞行共轭; 迁飞意愿; 表观调控; 迁飞与生殖

Insect migration behavior and its regulation

LIU Peng-Cheng^{1**} DIAO Yue-Hui¹ GUO Jia-Wen² GAO Bo-Ya¹ HU Gao^{1***}

(1. Department of Entomology, College of Plant Protection, Nanjing Agricultural University, Nanjing 210095, China;

2. Institute of Plant Protection and Microbiology, Zhejiang Academy of Agricultural Sciences, Hangzhou 310021, China)

Abstract Migration is a behavioral strategy that allows insects to respond to seasonal changes in resources and the environment. Insects not only escape adverse environmental conditions through migration, but their exceedingly high fecundity allows them to rapidly increase their population size on arrival in favorable new habitats, causing outbreaks that have a severe effect on both natural and agricultural ecosystems. Based on the concept of partial migration, this article firstly describes the differences in morphology, behavior, and physiology between migratory and resident insects, focusing on the relationship between migration and concomitant reproduction, as well as external environmental factors that induce migration. Finally, the authors review and summarize the progress in research on the molecular mechanisms regulating insect migratory behavior. From sensing adverse environmental signals to deciding to migrate, from take-off, flying and landing, to deciding to continue or terminate migration, the whole process largely depends on important internal factors, including endocrine and epigenetic regulatory factors. The underlying molecular mechanisms, however, require further investigation.

Key words partial migration; oogenesis-flight syndrome; migratory potential; epigenomic regulation; migration and reproduction

每年, 当数以亿万计的昆虫飞过天空, 寻找千里之外的繁殖之所, 以增加种群生存机会的时候, 也影响了整个自然生态系统和农业生态系统 (Dingle, 2014; Chapman *et al.*, 2015; Hu *et al.*, 2016)。规模如此宏大的昆虫迁飞, 或为爆发性农业害虫, 屡屡区域性大暴发, 小虫成大灾, 造

成损失触目惊心; 或为媒介昆虫, 造成人畜疾病或植物病害的流行和暴发 (Huestis *et al.*, 2019); 或为访花昆虫、天敌昆虫, 提供特定的生态服务 (Bauer and Hoyer, 2014; Wotton *et al.*, 2019; Satterfield *et al.*, 2020)。尽管如此, 目前大家对动物迁徙 (Migration) 仍没有统一的定义, 国际

*资助项目 Supported projects: 国家自然科学基金资助项目 (31822043)

**第一作者 First author, E-mail: pcliu@njau.edu.cn

***通讯作者 Corresponding author, E-mail: hugao@njau.edu.cn

收稿日期 Received: 2021-04-01; 接受日期 Accepted: 2021-05-02

上不少学者仍将动物迁徙局限于脊椎动物在“繁殖区”和“非繁殖区(比如越冬区)”之间的季节性往返运动。本文采用 Kennedy 和 Dingle 基于个体行为的定义,即:迁徙是指动物通过自身的迁移能力或者通过主动搭乘运载工具(风、水流等)来完成的一种持续、径直向外的运动,在此过程中部分日常活动行为(觅食或求偶)会被暂时抑制,但迁徙结束后会立即得到恢复甚至加强(Dingle, 2014; Chapman *et al.*, 2015)。该定义可以涵盖所有动物类群的迁徙行为,与迁徙距离、路线和方式没有必然联系。很显然,迁徙行为必然导致空间位置转移,但这可以理

解为是个体迁徙行为导致种群层次上生境的变化。换言之,迁徙定义为个体的行为过程,但需要从生态或进化水平上来解释该行为的功能和意义。

本文作者已从个体空中行为、种群时空动态和生态效应三个层次对迁飞昆虫学主要研究进展进行了综述(胡高等, 2020),同时近年来亦有多篇英文综述文章从不同角度阐述了昆虫迁飞的生态效应(Chapman *et al.*, 2015; Gao *et al.*, 2020; Satterfield *et al.*, 2020)。因此,本文仅围绕昆虫迁飞行为的过程(图 1),综述该行为生理基础和调控机制方面的研究进展。

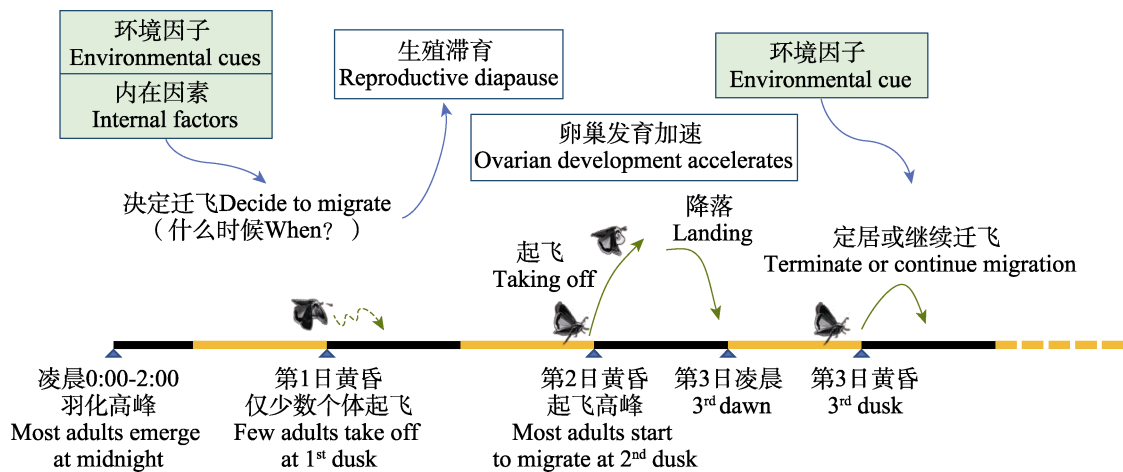


图 1 稻纵卷叶螟迁飞过程示意图

Fig. 1 Schematic diagram of the migration process of *Cnaphalocrocis medinalis*

稻纵卷叶螟成虫大多在凌晨 0:00-2:00 羽化,仅少数个体在 1 日龄开始迁飞外,大部分个体在 2 日龄日落后 0.5 h 内开始迁飞。稻纵卷叶螟是典型的采用多次经停迁飞模式的昆虫,即当天黄昏起飞后次日凌晨降落,次日黄昏再次起飞,可以连续飞行 3-5 个夜晚。昆虫决定迁飞、起飞、降落以及决定继续迁飞或终止迁飞等系列过程都受到外界环境因子、自身内因因素的影响,迁飞行为与生殖行为亦存在很强的耦合关系。

Cnaphalocrocis medinalis adults usually emerge at midnight (0:00-2:00), and most of them start to migrate within half an hour after sunset on the 2nd day but not 1st day post eclosion. *C. medinalis* is a typical insect that adopts a multi-stop migration mode. The nocturnal moth always takes off at dusk, stops flight at the next dawn, and takes off again at the next dusk. This long-distance migration can last 3-5 consecutive nights. From deciding to migrate, taking off, flying, landing, to finally deciding to terminate or continue further migrations, the whole processes of the insect migration largely depend on important external environmental cues and internal factors. More interestingly, migration behavior and reproduction behavior form a solid coupling relationship between each other.

1 部分迁飞: 迁飞型与居留型

部分迁飞(Partial migration)是指种群中部分个体居留,另一部分个体迁飞的现象(Menz *et al.*, 2019)。尽管该术语在昆虫迁飞研究中很少使用,但事实上绝大部分昆虫种类的迁飞均属

于部分迁飞(Menz *et al.*, 2019)。

部分迁飞反映了种群内部由于在生理、形态、行为上的差异导致不同个体在迁飞倾向上的差异,形成迁飞型个体和居留型个体。在褐飞虱 *Nilaparvata lugens*、马利筋长蝽 *Oncopeltus fasciatus* 等具有翅二型现象的迁飞昆虫中,其迁

飞型和居留型个体存在明显的形态差异: 成虫分为长翅型和短翅型。长翅型具有强飞行能力, 适合于远距离迁飞。与此同时, 其余大多数昆虫如蝇类、蝶类、蛾类和蜻蜓等的迁飞型个体和居留型个体之间并不存在翅型分化现象, 因此不存在肉眼可见的、明显的形态差异。然而, 有研究报告美国大斑蝶 *Danaus plexippus* 和南方大斑蝶 *D. erippus* 的迁飞个体具有比居留个体更大、更尖的翅以及较小的翅负荷(体重与翅面积之比), 其飞行效率也高于居留个体 (Dockx, 2007; Altizer and Davis, 2010; Slager and Malcolm, 2015; Vander Zanden *et al.*, 2018)。黑带食蚜蝇 *Episyrphus balteatus* 迁飞个体与本地越冬种群之间没有显著的翅形差异 (Raymond *et al.*, 2014)。

此外, 部分迁飞昆虫种类在形态上也存在明显的多型现象, 比如东方粘虫 *Mythimna separata*、非洲粘虫 *Spodoptera exempta* 的深色型和浅色型, 或者蝗虫的群居型和散居型, 但这种分型现象是否跟迁飞相关存在争论。蝗虫在英文文献中有 Grasshopper 和 Locust 的区分。Locust 特指具有非常典型的“种群密度相关的型变现象”的一类 Grasshopper, 如沙漠蝗 *Schistocerca gregaria*、东亚飞蝗 *Locusta migratoria*, 种群密度大时表现为群居型, 反之为散居型。群居型蝗群在白天进行远距离迁飞; 散居型个体也能够进行远距离迁飞, 但通常在夜间迁飞 (Chapman, 2009; Tu *et al.*, 2020)。亚洲小车蝗 *Oedaleus asiaticus* 并非 Locust, 但也存在与种群密度相关的深色型和浅色型的差异, 两者在体色、体长、后翅面积、后足股节长度上均有显著差异 (Cease *et al.*, 2010; 高书晶等, 2016), 但是飞行肌大小、脂类物质储存上没有明显差异 (Cease *et al.*, 2010); 罩笼观测发现虽然深色型个体的起飞比例要高于浅色型个体, 但两者的总体起飞比例都非常低 (Wang *et al.*, 2020a)。

2 迁飞行为与生殖

大多数研究者认为昆虫迁飞需要消耗大量能量, 飞行肌的发育以及飞行本身都需要大量能源物质投入, 从而导致生殖适合度的降低

(Tigreros and Davidowitz, 2019)。因此, 非迁飞昆虫(种类或个体)往往被认为比迁飞昆虫具有更高的繁殖力 (Menz *et al.*, 2019; Tigreros and Davidowitz, 2019)。但事实上, 相较于非迁飞昆虫种类, 迁飞昆虫可能具有更高的繁殖力。例如, 欧洲蛾类迁飞昆虫, 如丫形银纹夜蛾 *Autographa gamma*、小地老虎 *Agrotis ipsilon*、模夜蛾 *Noctua pronuba* 雌成虫的产卵量基本上都在 1 000-2 000 粒, 是相同个体大小的非迁飞蛾类昆虫平均产卵量的 4-5 倍 (Spitzer *et al.*, 1984)。对于同一物种来说, 迁飞个体的繁殖力也未必低于居留个体 (Tigreros and Davidowitz, 2019)。稻纵卷叶螟 *Cnaphalocrocis medinalis* 迁入种群雌成虫反而比本地居留种群交配次数更多, 产卵量更高 (杨帆等, 2013)。稻纵卷叶螟、草地螟 *Loxostege sticticalis*、草地贪夜蛾 *Spodoptera frugiperda* 等蛾类昆虫在 1-3 日龄经过一段时间的吊飞(一般单次吊飞不超过 12 h), 产卵量均没有显著减少 (Cheng *et al.*, 2012; Zhang *et al.*, 2015; Ge *et al.*, 2021)。不过, 翅二型昆虫(包括迁飞和非迁飞昆虫种类)长翅型雌成虫的产卵量通常少于短翅型个体 (Roff, 1986; Guerra, 2011)。但也有研究报告, 褐飞虱短翅型和长翅型雌成虫产卵量差异并不明显 (Manjunath, 1977)。

基于对自身有限能源物质的竞争, 迁飞和生殖之间往往在能量分配上形成一种权衡 (Trade-off)。非迁飞个体可以立即将资源投入生殖过程, 而迁飞个体往往会先通过生殖滞育将资源优先分配给飞行器官。这种权衡称为“卵子发生-飞行共轭” (Oogenesis-flight syndrome) (Johnson, 1963, 1969)。因此, 雌成虫的迁飞通常发生在产卵前期或者卵巢幼嫩期, 待迁飞结束之后卵巢才开始发育, 甚至有观点认为性成熟(卵巢发育成熟)意味着迁飞结束 (Zhao *et al.*, 2009)。翅二型昆虫的短翅型雌成虫通常具有较短的产卵前期; 长翅型产卵前期延长, 迁飞大多发生在产卵前期 (Roff, 1986; Guerra, 2011)。不具有翅型分化的迁飞蛾类通常进行多个夜晚的连续迁飞, 大多数雌成虫的迁飞也都开始于卵

巢幼嫩期。稻纵卷叶螟成虫 1-3 日龄没有补充营养时, 胸部能源物质甘油三酯含量一直维持稳定, 但腹部甘油三酯含量 3 日龄起开始下降, 表明稻纵卷叶螟迁飞个体可能优先为飞行器官提供能量 (Guo *et al.*, 2019)。田间采集的稻纵卷叶螟迁出代种群被迫滞留后, 其产卵前期显著延长, 产卵量只有迁入代种群和本地繁殖代种群的四分之一, 这也表明迁飞型个体在迁飞行为发生之前确实存在对生殖的抑制 (杨帆等, 2013)。但是迁飞行为发生之后, 飞行将促进蛾类昆虫卵巢发育, 产卵前期缩短, 产卵期更为集中和整齐, 性成熟也并不代表着迁飞终止 (Cheng *et al.*, 2012, 2016; Zhang *et al.*, 2015; Ge *et al.*, 2021)。稻纵卷叶螟雌成虫连续吊飞 3 个夜晚后, 大部分卵巢就已发育至成熟状态 (Zhang *et al.*, 2015; Wang *et al.*, 2017), 但大多数个体连续吊飞 4-5 个夜晚仍有非常强的飞行能力, 最长可达到 9 个夜晚 (王凤英等, 2010)。春季在渤海海峡中间的小岛上用高空探照灯所诱集的稻纵卷叶螟、东方粘虫、小地老虎 *Agrotis ipsilon*、黄地老虎 *A. segetum*、小菜蛾 *Plutella xylostella* 等蛾类均为空中正在迁飞的成虫, 大多数雌成虫卵巢已发育成熟, 并且已经完成交配 (Zhao *et al.*, 2009; Fu *et al.*, 2014a, 2014b; Guo *et al.*, 2015; Liu *et al.*, 2015a)。此外, 还有部分昆虫种类雌成虫迁飞前卵巢已发育完全, 如甜菜夜蛾 *S. exigua* (Han *et al.*, 2008; Jiang *et al.*, 2010)、峻伟蛱 *Anax junius* (May *et al.*, 2017)。总而言之, 目前对“卵子发生-飞行共轭”理论仍存在一定的争议。

尽管迁飞未必导致昆虫生殖适合度的降低, 但对于大多数迁飞昆虫种类来说, 迁飞行为是在卵巢幼嫩阶段启动的, 迁飞行为发生之前存在生殖滞育现象。昆虫之所以迁飞通常是因为面临正在恶化的生境, 因此迁飞之前的生殖滞育可以让昆虫避免在当前正在恶化的生境中产卵繁殖后代。迁飞行为启动之后, 卵巢发育加快, 产卵期提前可能有利于种群快速定殖, 并通过迁飞占领更广的生境。因此, 性成熟甚至产卵繁殖可能并不会导致迁飞行为的结束。

3 诱导昆虫迁飞的环境因子及其关键敏感期

迁飞是昆虫应对不良环境的一种生活史策略。种群密度增加、食料条件恶化、天敌和病原微生物数量上升以及光照、温度等外界环境因子的改变都可能导致当前生境综合性恶化, 从而诱导昆虫迁飞行为的发生 (Chapman *et al.*, 2015; Menz *et al.*, 2019)。

对于稻飞虱、蚜虫、蟋蟀等存在翅型分化的昆虫, 翅的形态一般在若虫期就已决定。褐飞虱 3 龄若虫是翅分化的关键期, 拥挤与否和寄主植物营养条件是翅分化最为主要的环境诱导因子 (Lin *et al.*, 2018); 蚜虫属于胎生, 子蚜可通过母蚜感知环境变化来决定翅的形态, 通过触觉感知拥挤导致长翅蚜大量形成。Zhang 等 (2019) 对翅二型昆虫进行了详细综述, 这里不再赘述。

对于不存在翅型分化的迁飞昆虫, 不论迁飞个体还是居留个体都拥有实现飞行的器官。幼虫期种群密度增加或食料条件恶化是否导致成虫迁飞尚无明确结论, 或者在不同昆虫中存在差异。在高密度饲养条件下, 非洲粘虫强飞行个体 (持续飞行时间较长的个体) 的比例显著增加, 个体甘油三酯含量相应增加 (Parker and Gatehouse, 1985), 而且其后代也具有更强的飞行能力 (Woodrow *et al.*, 1987)。但是东方粘虫和草地螟仅在中等密度条件下, 强飞行个体的比例才显著增加 (罗礼智等, 1995; Kong *et al.*, 2010), 而稻纵卷叶螟幼虫期拥挤对成虫迁飞没有影响 (Yang *et al.*, 2015)。其中草地螟在中等密度条件下, 产卵前期最长, 个体甘油三酯含量最高 (Kong *et al.*, 2010)。幼虫期采用不同食料条件饲养可显著影响东方粘虫、非洲粘虫、稻纵卷叶螟等的幼虫发育历期、蛹发育历期、蛹重, 但对非洲粘虫、东方粘虫的强飞行个体比例, 稻纵卷叶螟雌成虫的产卵前期均无显著影响 (张孝羲等, 1981; Parker and Gatehouse, 1985; 曹雅忠等, 1996; Yang *et al.*, 2015)。但也有研究发现稻纵卷叶螟 1-4 龄幼虫期在叶鞘部位取食的雌成虫卵巢发育要显著迟于整个幼虫期取食叶片

的雌成虫(吴进才, 1985)。不过, 由于食料材料和种群密度均会直接影响昆虫发育和能量积累, 产卵前期延长可能是源于营养条件不足而导致的发育延迟, 个体持续飞行时间短也可能是源于营养条件不足而导致的前期能量积累不足, 因此, 产卵前期、个体持续飞行时间并不能完全反映昆虫真正的迁飞倾向。

对于不存在翅型分化的迁飞昆虫, 光照周期和温度变化在一定条件下能够诱导成虫迁飞(Han and Gatehouse, 1991; Hill and Gatehouse, 1992; Zhou et al., 2000)。例如, 稻纵卷叶螟春夏季(或长光照条件下)经历逐渐上升的高温将导致成虫卵巢发育延迟, 而秋季光照逐渐缩短是诱导其南迁的主要因素(张孝羲等, 1981; 吴进才, 1985)。一点粘虫 *Pseudaletia unipuncta*、东方粘虫的相关研究进一步表明, 光周期和温度变化诱导成虫迁飞的敏感时期为预蛹期或成虫羽化初期(Delisle and McNeil, 1986, 1987; Han and Gatehouse, 1991; 曹雅忠等, 1997)。此外, 成虫期补充营养情况也能影响迁飞行为发生。在 1 日龄饥饿的稻纵卷叶螟成虫, 其他日龄无论是否补充营养, 其个体起飞比例大幅度增加, 产卵前期延长; 但如果仅在 1 日龄饥饿(其他日龄正常饲喂), 其雌虫交配率、产卵量、飞行能力均没有显著影响; 相反, 其他日龄饥饿的成虫起飞比例不受影响(Guo et al., 2019)。迁飞型东方粘虫 1 日龄饥饿后, 72 h 以内飞行肌和飞行能力跟未饥饿的对照组没有显著差异, 但产卵前期大幅度缩短、卵巢发育提前, 说明 1 日龄饥饿导致东方粘虫从迁飞型转变为居留型(张蕾等, 2006; Zhang et al., 2008a, 2018b)。不过, 成虫通过蜜源植物来补充营养, 而迁飞是为子代寻找合适的生境, 蜜源植物的有无多寡跟子代适宜生境并不存在必然联系。因此, 尽管稻纵卷叶螟和东方粘虫的研究结论存在差异, 但这都表明成虫羽化初期是成虫决定是否迁飞的关键时期。

4 昆虫迁飞行为调控的分子机制

对于存在翅型分化的昆虫, 翅型差异意味着迁飞型和居留型的区别, 迁飞行为分子机制的研

究也因此主要集中在翅型分化上(Zhang et al., 2019)。无论是昆虫种群密度增加, 还是寄主植物营养条件恶化, 都会直接或间接地导致昆虫营养摄取不足。因此, 昆虫翅型分化必然与昆虫感受营养的信号转导通路相关。其中胰岛素通路主要感受各种糖和环境压力等变化的信号, 近年来被证实与多数昆虫的翅型分化相关, 如褐飞虱(Xu et al., 2015; Lin et al., 2016a, 2016b, 2018; Zhang et al., 2019)、褐色桔蚜 *Aphis citricidus* 和豌豆蚜 *Acyrtosiphon pisum*(Shang et al., 2020) 以及红肩美姬缘蝽 *Jadera haematoloma*(Fawcett et al., 2018)。以褐飞虱为例, 两个胰岛素受体 InR1 和 InR2 通过调节叉头基因 FOXO 的活性控制其翅型发育。具体来说, 不良环境诱导分泌性脑细胞分泌胰岛素样肽(Insulin-like peptides, ILPs), 胰岛素样肽作用于翅芽部位的胰岛素受体。InR1 通过激活 PI3K-Akt 信号级联导致长翅型个体, 而 InR2 是该途径的负调节剂, 抑制胰岛素信号通路, 导致短翅型个体产生(Xu et al., 2015; Zhang et al., 2019)。此外, 也有研究表明蜕皮激素和保幼激素参与了翅型分化的调控过程(Roff and Fairbairn, 2007; Vellichirammal et al., 2017), 详见 Zhang 等(2019)关于翅型分化分子机制的综述。

翅型分化是昆虫因响应不同环境信号而产生不同的表型。除了内分泌调控因子之外 microRNA 也被证实参与翅型分化的调控。microRNA 通过抑制蛋白质的翻译来调节基因表达, 在表观调控中具有重要作用。褐色桔蚜在拥挤环境下会下调 miR-9b 基因的表达, 使得 ABC 转运蛋白(AcABCG4)上调, 从而激活胰岛素信号通路, 产生高比例的有翅后代(Shang et al., 2020)。Ye 等(2019)在褐飞虱体内也发现了一个 mircoRNA(miR-34)能够与胰岛素通路、保幼激素、蜕皮激素等形成一个正向调控回路, 协同调控褐飞虱的翅型分化。

由于昆虫迁飞与生殖存在非常强的耦合关系, 而且保幼激素与生殖调控密切相关(Santos et al., 2019), 因此早期研究认为保幼激素的滴度变化决定了昆虫迁飞还是居留。通常认为低滴

度的保幼激素有利于昆虫迁飞 (Rankin and Riddiford, 1978; Roff and Fairbairn, 2007)。东方粘虫居留型个体中保幼激素滴度显著高于迁飞型个体, 利用保幼激素类似物处理 1 日龄雌成虫显著增加其繁殖能力并抑制其飞行能力, 导致迁飞型个体转变为居留型 (Zhang *et al.*, 2020)。东方粘虫和一点粘虫的促咽侧体素基因 mRNA 表达量与保幼激素水平成正相关, 在羽化初期 (0-1 日龄) 注射促咽侧体素可促使迁飞型个体居留繁殖 (McNeil *et al.*, 2005; Jiang *et al.*, 2011), 这不仅表明保幼激素可能参与迁飞与生殖的协同调控, 也表明羽化初期是鳞翅目昆虫决定迁飞的关键敏感期。在棉铃虫 *Helicoverpa armigera* 具有长距离飞行能力的个体中, 促咽侧体素受体 (*BNGR-A16*) 的表达显著下调 (Jones *et al.*, 2015)。尽管上述研究证实了保幼激素在调控迁飞行为中具有关键作用, 而保幼激素调控生殖的分子机制在多种非迁飞性昆虫中均有深入研究 (Liu *et al.*, 2015b, 2018; Santos *et al.*, 2019), 但是迁飞与生殖之间详细的内分泌交互调控机制仍不清楚。此外, Guo 等 (2020) 报道了聚集信息素 4-乙烯基苯甲醚诱导飞蝗产生一系列电生理和行为学反应, 从而调控飞蝗型变的发生, 其中关于基因调控和表观遗传调控的研究对后续阐释昆虫迁飞行为诱导的分子机理提供了较好的借鉴。除此之外, 昆虫迁飞过程通常持续数个小时, 因此需要高效的运输系统来主动维持飞行动力; 并且不少昆虫具有较强的定向能力, 而昆虫迁飞行为本身也具有很强的节律性 (如春季北迁, 秋季南迁; 夜间迁飞昆虫日落时刻起飞等) (胡高等, 2020)。因此, 迁飞行为是一个非常复杂的过程, 其调控必然也涉及到能量代谢、定向机制以及节律调控等。Jones 等 (2015) 通过对飞行距离存在显著差异的棉铃虫种群进行转录组分析, 发现表达水平有差异的基因主要涉及脂类能量物质转运、飞行肌发育和激素调节等信号通路。其中, 气味结合蛋白 OBP6 在希腊种群和中国种群中具有远距离迁飞能力的个体中均显著高表达。进一步研究发现气味结合蛋白 (OBP) 的疏水配体能够高效结合脂类能量物质

从而支持昆虫的飞行活动, 其作用超出了它们在嗅觉系统中的典型功能 (Wang *et al.*, 2020b)。最新研究发现, 帝王蝶依赖 UV-A/蓝光波段和 I 型隐花色素蛋白 (CRY1) 响应地球磁场磁倾角的变化, 触角和复眼等重要器官高度表达 CRY1, 行使磁感受功能 (Wan *et al.*, 2021)。鉴于本综述的重点仅是迁飞行为生理调控的分子机制, 而能量代谢、定向机制以及节律行为都是昆虫学甚至于动物学的重要研究方向, 这里不做深入展开和讨论。

5 结语

昆虫利用迁飞逃避不良环境, 同时其强大的繁殖力确保种群在短时间内实现快速增长最终暴发成灾。迁飞性昆虫对自然生态系统以及农业生态系统具有极其重要的影响, 其为害也远甚于其他害虫。因此, 明确昆虫迁飞行为的生理与分子调控机制, 可为迁飞性昆虫的科学管理提供新的思路。江幸福和罗礼智 (2008) 在其综述中写道: “从 20 世纪 50 年代起, 尽管国内外昆虫学家致力于昆虫迁飞行为机制研究, 但不可否认, 有关昆虫起飞、飞行与降落三个阶段行为调控的生理学、细胞学和分子机制仍未能取得重大突破。”然而, 近年来除了在昆虫翅型分化的分子机制研究方面取得突破外, 其他方面仍未能有实质性进展。

首先, 昆虫种群密度、寄主植物营养状况、光照和温度等外部环境条件都可能诱导昆虫迁飞行为的发生。从已有研究报道来看, 大致可分为营养感受类、光照温度类环境信号 (与季节节律相关) 两类。但对于大多数昆虫来说, 诱导昆虫迁飞的关键环境因子是什么仍不清楚。有重要决定作用的内在因素亦不明确。昆虫何时决定迁飞, 即迁飞关键敏感期更不清楚。对于翅型分化的昆虫来说, 有翅或者长翅仅表明该个体具有远距离迁飞的器官和能力, 并非意味着该个体一定会迁飞。从感受到不良环境信号到决定迁飞这一过程中, 信号感知、信号传导以及信号表达等一系列的生理和分子机制更不明确。

其次, 昆虫做出迁飞决定之后, 如何快速高

效地调动自身神经信号、内分泌信号和动力系统（肌肉或能量），最终促成了起飞行为的发生，并持续维持其飞行行为？亚洲小车蝗起飞前会排空消化道来减轻体重，同时其迁飞比例与温度和风速显著相关（Wang *et al.*, 2020a），这意味着昆虫起飞之前需要一系列的准备活动。更普遍的是，大多数迁飞昆虫在起飞行为发生之前存在明显的生殖滞育或发育迟缓，迁飞行为发生之后生殖过程受到促进，因此，迁飞与生殖二者如何交互调控？

最后，迁飞行为如何终止？目前对此研究鲜有报道。哪些外部环境因素或内在生理状态起关键调控作用，以及此类因素如何协同调控迁飞行为终止需要深入研究。此外，有研究表明，性成熟甚至产卵行为并不导致迁飞行为终止，这也对经典的“卵子发生与飞行共轭理论”提出了新的挑战。

参考文献 (References)

- Altizer S, Davis AK, 2010. Populations of monarch butterflies with different migratory behaviors show divergence in wing morphology. *Evolution*, 64(4): 1018–1028.
- Bauer S, Hoyer BJ, 2014. Migratory animals couple biodiversity and ecosystem function worldwide. *Science*, 344(6179): 1242552.
- Cao YZ, Li GB, Hu Y, 1997. Effect of photoperiod on reproduction and flight of oriental armyworm *Mythimna separata* (Walker). *Acta Ecologica Sinica*, 17(4): 402–406. [曹雅忠, 李光博, 胡毅, 1997. 光周期对粘虫生殖与飞翔影响的初步研究. *生态学报*, 17(4): 402–406.]
- Cao YZ, Luo YL, Guo J, 1996. Performance of adult reproduction and flight in relation to larval nutrition in the oriental armyworm, *Mythimna separata* (Walker). *Acta Entomologica Sinica*, 39(1): 105–108. [曹雅忠, 罗礼智, 郭军, 1996. 粘虫生殖和飞翔与幼虫期营养的关系. *昆虫学报*, 39(1): 105–108.]
- Cease AJ, Hao S, Kang L, Elser JJ, Harrison JF, 2010. Are color or high rearing density related to migratory polyphenism in the band-winged grasshopper *Oedaleus asiaticus*? *Journal of Insect Physiology*, 56(8): 926–936.
- Chapman JW, Reynolds DR, Wilson K, 2015. Long-range seasonal migration in insects: Mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters*, 18(3): 287–302.
- Chapman RF, 2009. Locusts//Resh VH, Cardé RT (eds.). *Encyclopedia of Insects* (2nd version). Academic Press. 589–591.
- Cheng Y, Luo L, Sappington TW, Jiang X, Zhang L, Frolov AN, 2016. Onset of oviposition triggers abrupt reduction in migratory flight behavior and flight muscle in the female beet webworm, *Loxostege sticticalis*. *PLoS ONE*, 11(11): e0166859.
- Cheng YX, Luo LZ, Jiang XF, Sappington TW, 2012. Synchronized oviposition triggered by migratory flight intensifies larval outbreaks of beet webworm. *PLoS ONE*, 7(2): e31562.
- Delisle J, McNeil JN, 1986. The effect of photoperiod on the calling behaviour of virgin females of the true armyworm *Pseudaletia unipuncta* (Haw.) (Lepidoptera: Noctuidae). *Journal of Insect Physiology*, 32(3): 199–206.
- Delisle J, McNeil JN, 1987. The combined effect of photoperiod and temperature on the calling behaviour of the true armyworm *Pseudaletia unipuncta*. *Physiological Entomology*, 12(2): 157–164.
- Dingle H, 2014. *Migration: The Biology of Life on the Move* (2nd Edition). New York: Oxford University Press. 1–747.
- Dockx C, 2007. Directional and stabilizing selection on wing size and shape in migrant and resident monarch butterflies, *Danaus plexippus* (L.), in Cuba. *Biological Journal of the Linnean Society*, 92(4): 605–616.
- Fawcett MM, Parks MC, Tibbetts AW, Swart JS, Richards EM, Vanegas JC, Censer M, Crowley L, Simmons WR, Hou WS, Angelini DR, 2018. Manipulation of insulin signaling phenocopies evolution of a host-associated polyphenism. *Nature Communications*, 9(1): 1699.
- Fu X, Xing Z, Liu Z, Ali A, Wu KM, 2014a. Migration of diamondback moth, *Plutella xylostella*, across the Bohai Sea in northern China. *Crop Protection*, 64: 143–149.
- Fu XW, Li C, Feng HQ, Liu ZF, Chapman JW, Reynolds DR, Wu KM, 2014b. Seasonal migration of *Cnaphalocrocis medinalis* (Lepidoptera: Crambidae) over the Bohai Sea in northern China. *Bulletin of Entomological Research*, 104(5): 601–609.
- Gao B, Hedlund JSU, Reynolds DR, Zhai BP, Hu G, Chapman JW, 2020. The 'migratory connectivity' concept, and its applicability to insect migrants. *Movement Ecology*, 8(1): 48.
- Gao SJ, Han HB, Wang N, Xu LB, Liu AP, Temuer, 2016. Morphometric analyses of gregarious and solitary phases of *Oedaleus decorus asiaticus*. *Plant Protection*, 42(4): 89–93. [高书晶, 韩海斌, 王宁, 徐林波, 刘爱萍, 特木尔, 2016. 群居型、散居型亚洲小车蝗形态特征的数量分析. *植物保护*, 42(4): 89–93.]
- Ge SH, He W, He LM, Yan R, Zhang HW, Wu KM, 2021. Flight activity promotes reproductive processes in the fall armyworm, *Spodoptera frugiperda*. *Journal of Integrative Agriculture*, 20(3): 727–735.

- Guerra PA, 2011. Evaluating the life-history trade-off between dispersal capability and reproduction in wing dimorphic insects: A meta-analysis. *Biological Reviews*, 86(4): 813–835.
- Guo JL, Fu XW, Wu X, Zhao XC, Wu KM, 2015. Annual migration of *Agrotis segetum* (Lepidoptera: Noctuidae): Observed on a small isolated island in northern China. *PLoS ONE*, 10(6): e0131639.
- Guo JW, Li P, Zhang J, Liu XD, Zhai BP, Hu G, 2019. *Cnaphalocrocis medinalis* moths decide to migrate when suffering nutrient shortage on the first day after emergence. *Insects*, 10(10): 364.
- Guo XJ, Yu QQ, Chen DF, Wei JN, Yang PC, Yu J, Wang XH, Kang L, 2020. 4-Vinylanisole is an aggregation pheromone in locusts. *Nature*, 584(7822): 1–5.
- Han EN, Gatehouse AG, 1991. Effect of temperature and photoperiod on the calling behaviour of a migratory insect, the oriental armyworm *Mythimna separata*. *Physiological Entomology*, 16(4): 419–427.
- Han LZ, Gu HN, Zhai BP, Zhang XX, 2008. Reproduction-flight relationship in the beet armyworm, *Spodoptera exigua* (Lepidoptera: Noctuidae). *Environmental Entomology*, 37(2): 374–381.
- Hill JK, Gatehouse, 1992. Effects of temperature and photoperiod on development and pre-reproductive period of the silver Y moth *Autographa gamma* (Lepidoptera: Noctuidae). *Bulletin of Entomological Research*, 82(3): 335–341.
- Hu G, Gao BY, Feng HQ, Jiang XF, Zhai BP, Wu KM, 2020. Insect migration: Individual behaviour, population dynamics and ecological consequences. *Bulletin of National Natural Science Foundation of China*, 34(4): 456–463. [胡高, 高博雅, 封洪强, 江幸福, 翟保平, 吴孔明, 2020. 迁飞昆虫的个体行为、种群动态及生态效应. 中国科学基金, 34(4): 456–463.]
- Hu G, Lim KS, Horvitz N, Clark SJ, Reynolds DR, Sapir N, Chapman JW, 2016. Mass seasonal bioflows of high-flying insect migrants. *Science*, 354(6319): 1584–1587.
- Huestis DL, Dao A, Diallo M, Sanogo ZL, Samake ASY, Ousman Y, Linton YM, Krishna A, Veru L, Krajacich BJ, Faiman R, Florio J, Chapman JW, Reynolds DR, Weetman D, Mitchell R, Donnelly MJ, Talamas E, Chamorro L, Strobach E, Lehmann T, 2019. Windborne long-distance migration of malaria mosquitoes in the Sahel. *Nature*, 574(7778): 404–408.
- Jiang X, Luo L, Zhang L, Sappington TW, Hu Y, 2011. Regulation of migration in *Mythimna separata* (Walker) in China: A review integrating environmental, physiological, hormonal, genetic, and molecular factors. *Environmental Entomology*, 40(3): 516–533.
- Jiang XF, Luo LZ, Sappington TW, 2010. Relationship of flight and reproduction in beet armyworm, *Spodoptera exigua* (Lepidoptera: Noctuidae), a migrant lacking the oogenesis-flight syndrome. *Journal of Insect Physiology*, 56(11): 1631–1637.
- Jiang XF, Luo LZ, 2008. Regulation basis and perspectives on insect migration. *Acta Ecologica Sinica*, 28(6): 2835–2842. [江幸福, 罗礼智, 2008. 昆虫迁飞的调控基础及其展望. 生态学报, 28(6): 2835–2842.]
- Johnson CG, 1963. Physiological factors in insect migration by flight. *Nature*, 198(4879): 423–427.
- Johnson CG, 1969. Migration and Dispersal of Insects by Flight. London: Methuen. 1–766.
- Jones CM, Papanicolaou A, Mironidis GK, Vontas J, Yang Y, Lim KS, Oakeshott JG, Bass C, Chapman JW, 2015. Genomewide transcriptional signatures of migratory flight activity in a globally invasive insect pest. *Molecular Ecology*, 24(19): 4901–4911.
- Kong H, Luo L, Jiang X, Zhang L, 2010. Effects of larval density on flight potential of the beet webworm, *Loxostege sticticalis* (Lepidoptera: Pyralidae). *Environmental Entomology*, 39(5): 1579–1585.
- Lin X, Xu Y, Jiang J, Lavine M, Lavine LC, 2018. Host quality induces phenotypic plasticity in a wing polyphenic insect. *Proceedings of the National Academy of Sciences of the United States of America*, 115(29): 7563–7568.
- Lin X, Xu Y, Yao Y, Wang B, Lavine MD, Lavine LC, 2016a. JNK signaling mediates wing form polymorphism in brown planthoppers (*Nilaparvata lugens*). *Insect Biochemistry & Molecular Biology*, 73: 55–61.
- Lin X, Yao Y, Wang B, Emlen DJ, Lavine LC, 2016b. Ecological trade-offs between migration and reproduction are mediated by the nutrition-sensitive insulin-signaling pathway. *International Journal of Biological Sciences*, 12(5): 607–616.
- Liu P, Fu X, Zhu J, 2018. Juvenile hormone-regulated alternative splicing of the taiman gene primes the ecdysteroid response in adult mosquitoes. *Proceedings of the National Academy of Sciences of the United States of America*, 115(33): E7738–E7747.
- Liu P, Peng HJ, Zhu J, 2015b. Juvenile hormone-activated phospholipase C pathway enhances transcriptional activation by the methoprene-tolerant protein. *Proceedings of the National Academy of Sciences of the United States of America*, 112(15): E1871–E1879.
- Liu Y, Fu X, Feng H, Liu Z, Wu KM, 2015a. Trans-regional migration of *Agrotis ipsilon* (Lepidoptera: Noctuidae) in North-East Asia. *Annals of the Entomological Society of America*, 108(4): 519–527.

- Luo L, Li G, Cao Y, Hu Y, 1995. The influence of larval rearing density on flight capacity and fecundity of adult oriental armyworm, *Mythimna separata* (Walker). *Acta Entomologica Sinica*, 38(1): 38–45. [罗礼智, 李光博, 曹雅忠, 胡毅, 1995. 粘虫幼虫密度对成虫飞行与生殖的影响. 昆虫学报, 38(1): 38–45.]
- Manjunath TM, 1977. A note on oviposition in the macropterous and brachypterous forms of the rice brown planthopper, *Nilaparvata lugens* Stål (Homoptera, Delphacidae). *Proceedings of the Indian Academy of Sciences-Section B*, 86(6): 405–408.
- May ML, Gregoire JA, Gregoire SM, Lubertazzi MA, Matthews JH, 2017. Emergence phenology, uncertainty, and the evolution of migratory behavior in *Anax junius* (Odonata: Aeshnidae). *PLoS ONE*, 12 (9): e0183508.
- McNeil JN, Maury M, Bernier-Cardou M, Cusson M, 2005. *Manduca sexta* allatotropin and the in vitro biosynthesis of juvenile hormone by moth corpora allata: A comparison of *Pseudaletia unipuncta* females from two natural populations and two selected lines. *Journal of Insect Physiology*, 51(1): 55–60.
- Menz MHM, Reynolds DR, Gao B, Hu G, Chapman JW, Wotton KR, 2019. Mechanisms and consequences of partial migration in insects. *Frontiers in Ecology and Evolution*, 7: 403.
- Parker WE, Gatehouse AG, 1985. The effect of larval rearing conditions on flight performance in females of the African armyworm *Spodoptera exempta* (Walker) (Lepidoptera. Noctuidae). *Bulletin of Entomological Research*, 75 (1): 35–47.
- Rankin MA, Riddiford LM, 1978. Significance of haemolymph juvenile hormone titer changes in timing of migration and reproduction in adult *Oncopeltus fasciatus*. *Journal of Insect Physiology*, 24 (1): 31–38.
- Raymond L, Vialatte A, Plantegenest M, 2014. Combination of morphometric and isotopic tools for studying spring migration dynamics in *Episyrphus balteatus*. *Ecosphere*, 7(5): 88.
- Roff DA, Fairbairn DJ, 2007. The evolution and genetics of migration in insects. *BioScience*, 57 (2): 155–164.
- Roff DA, 1986. The evolution of wing dimorphism in insects. *Evolution*, 40(5): 1009–1020.
- Santos CG, Humann FC, Hartfelder K, 2019. Juvenile hormone signaling in insect oogenesis. *Current Opinion in Insect Science*, 31: 43–48.
- Satterfield DA, Sillett TS, Chapman JW, Altizer S, Marra PP, 2020. Seasonal insect migrations: Massive, influential, and overlooked. *Frontiers in Ecology and the Environment*, 18(6): 335–344.
- Shang F, Niu J, Ding BY, Zhang W, We DD, Wei D, Jiang HB, Wang JJ, 2020. The miR-9b microRNA mediates dimorphism and development of wing in aphids. *Proceedings of the National Academy of Sciences of the United States of America*, 117(15): 201919204.
- Slager BH, Malcolm SB, 2015. Evidence for partial migration in the southern monarch butterfly, *Danaus erippus*, in Bolivia and Argentina. *Biotropica*, 47(3): 355–362.
- Spitzer K, Rejmánek M, Soldán T, 1984. The fecundity and long-term variability in abundance of noctuid moths (Lepidoptera, Noctuidae). *Oecologia*, 62(1): 91–93.
- Tigreros N, Davidowitz, 2019. Flight-fecundity tradeoffs in wing-monomorphic insects. *Advances in Insect Physiology*, 56: 1–41.
- Tu X, Hu G, Fu X, Zhang Y, Ma J, Wang Y, Gould PJJ, Du G, Su H, Zhang Z, Chapman JW, 2020. Mass windborne migrations extend the range of the migratory locust in east China. *Agricultural and Forest Entomology*, 22(1): 41–49.
- Vander Zanden HB, Chaffee CL, González-Rodríguez A, Flockhart DTT, Norris DR, Wayne ML, 2018. Alternate migration strategies of eastern monarch butterflies revealed by stable isotopes. *Animal Migration*, 5(1): 74–83.
- Vellichirammal NN, Gupta P, Hall TA, Brisson JA, 2017. Ecdysone signaling underlies the pea aphid transgenerational wing polyphenism. *Proceedings of the National Academy of Sciences of the United States of America*, 114(6): 1419–1423.
- Wan G, Hayden AN, Iiams SE, Merlin C, 2021. Cryptochrome 1 mediates light-dependent inclination magnetosensing in monarch butterflies. *Nature Communications*, 12(1): 771.
- Wang FY, Yang F, Lu MH, Luo SY, Zhai BP, Lim KS, McInerney CE, Hu G, 2017. Determining the migration duration of rice leaf folder (*Cnaphalocrocis medinalis* Guenée) moths using a trajectory analytical approach. *Scientific Reports*, 7: 39853.
- Wang FY, Zhang XX, Zhai BP, 2010. Flight and re-migration capacity of the rice leaf folder moth, *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Crambidae). *Acta Entomologica Sinica*, 53(11): 1265–1272. [王凤英, 张孝羲, 翟保平, 2010. 稻纵卷叶螟的飞行和再迁飞能力. 昆虫学报, 53(11): 1265–1272.]
- Wang S, Minter M, Homem RA, Michaelson LV, Venthur H, Lim KS, Withers A, Xi J, Jones CM, Zhou JJ, 2020a. Odorant binding proteins promote flight activity in the migratory insect, *Helicoverpa armigera*. *Molecular Ecology*, 29(19): 3795–3808.
- Wang YP, Tu XB, Lin PJ, Li S, Xu CM, Wang XQ, Reynolds DR, Chapman JW, Zhang ZH, Hu G, 2020b. Migratory take-off behaviour of the Mongolian grasshopper *Oedaleus asiaticus*. *Insects*, 11(7): 416.
- Woodrow KP, Gatehouse AG, Davies DA, 1987. The effect of larval phase on flight performance of African armyworm moths, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). *Bulletin of Entomological Research*, 77(1): 113–122.

- Wotton KR, Gao B, Menz MHM, Morris RKA, Ball SG, Lim KS, Reynolds DR, Hu G, Chapman JW, 2019. Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services. *Current Biology*, 29(13): 1–7.
- Wu JC, 1985. Effect of change photoperiod, temperature and food quality on the migration rice leaf roller *Cnaphalocrocis Medinalis* Guenée. *Acta Entomologica Sinica*, 28(4): 398–405. [吴进才, 1985. 光照、温度及食物的变化对稻纵卷叶螟迁飞的效应. 昆虫学报, 28(4): 398–405.]
- Xu HJ, Xue J, Lu B, Zhang XC, Zhuo JC, He SF, Ma XF, Jiang YQ, Fan HW, Xu JY, Ye YX, Pan PL, Li Q, Bao YY, Nijhout HF, Zhang CX, 2015. Two insulin receptors determine alternative wing morphs in planthoppers. *Nature*, 519(7544): 464.
- Yang F, Hu G, Shi JJ, Zhai BP, 2015. Effects of larval density and food stress on life-history traits of *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae). *Journal of Applied Entomology*, 139(5): 370–380.
- Yang F, Zheng DB, Shi JJ, Hu G, Zhang XX, Zhai BP, 2013. Observations on migratory behavior of *Cnaphalocrocis medinalis*: When will they take-off? *Chinese Journal of Applied Entomology*, 50(3): 592–600. [杨帆, 郑大兵, 史金剑, 胡高, 张孝羲, 翟保平. 2013. 稻纵卷叶螟的起飞日龄观测. 应用昆虫学报, 50(3): 592–600.]
- Ye X, Xu L, Li X, He K, Hua H, Cao Z, Xu J, Ye W, Zhang J, Yuan Z, Li F, 2019. miR-34 modulates wing polyphenism in planthopper. *PLoS Genetics*, 15(6): e1008235.
- Zhang CX, Brisson JA, Xu HJ, 2019. Molecular mechanisms of wing polymorphism in insects. *Annual Review of Entomology*, 64: 297–314.
- Zhang L, Cheng L, Chapman JW, Sappington TW, Liu J, Cheng Y, Jiang X, 2020. Juvenile hormone regulates the shift from migrants to residents in adult oriental armyworm, *Mythimna separata*. *Scientific Reports*, 10(1): 11626.
- Zhang L, Jiang XF, Luo LZ, 2008a. Determination of sensitive stage for switching migrant oriental armyworms into residents. *Environmental Entomology*, 37(6): 1389–1395.
- Zhang L, Luo LZ, Jiang XF, Hu Y, 2006. Influences of starvation on the first day after emergence on ovarian development and flight potential in adults of the oriental armyworm, *Mythimna separata* (Walker) (Lepidoptera: Noctuidae). *Acta Entomologica Sinica*, 49(6): 895–902. [张蕾, 罗礼智, 江幸福, 胡毅, 2006. 一日龄饥饿对粘虫成虫卵巢发育和飞行能力的影响. 昆虫学报, 49(6): 895–902.]
- Zhang L, Luo LZ, Jiang XF, 2008b. Starvation influences allatotropin gene expression and juvenile hormone titer in the female adult oriental armyworm, *Mythimna separata*. *Archives of Insect Biochemistry and Physiology*, 68(2): 63–70.
- Zhang L, Pan P, Sappington TW, Lu W, Luo L, Jiang X, 2015. Accelerated and synchronized oviposition induced by flight of young females may intensify larval outbreaks of the rice leaf roller. *PLoS ONE*, 10(3): e0121821.
- Zhang XX, Geng JG, Zhou WJ, 1981. A study on ecological mechanism of the migration of rice leaf roller *Cnaphalocrocis medinalis*. *Journal of Nanjing Agricultural College*, 4(4): 40–51. [张孝羲, 耿济国, 周威君, 1981. 稻纵卷叶螟迁飞的生态机制研究. 南京农学院学报, 4(4): 40–51.]
- Zhao XC, Feng HQ, Wu B, Wu XF, Liu ZF, Wu KM, McNeil JN, 2009. Does the onset of sexual maturation terminate the expression of migratory behaviour in moths? A study of the oriental armyworm, *Mythimna separata*. *Journal of Insect Physiology*, 55(11): 1039–1043.
- Zhou X, Coll M, Applebaum, 2000. Effect of temperature and photoperiod on juvenile hormone biosynthesis and sexual maturation in the cotton bollworm, *Helicoverpa armigera*: implications for life history traits. *Insect Biochemistry and Molecular Biology*, 30(8/9): 863–868.