

昆虫聚集行为研究进展*

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摘 要 在动物界, 同种个体聚集现象较为普遍。聚集是昆虫适应环境变化、趋利避害的一种适应性策略。昆虫聚集行为的产生机制繁杂多样, 多数学者认为环境异质性和昆虫个体之间的交流互动可导致昆虫聚集行为的产生, 但其交流互动的内在机制的相关内容研究较少, 主要集中在化学信号的传递和识别等方面。近 20 年来, 有关昆虫聚集行为的研究逐渐深入, 本文总结了 20 世纪 70 年代至今国内外关于昆虫聚集行为的研究成果, 涉及聚集模式、聚集机制、聚集功能和意义以及适应性进化等研究, 为今后研究昆虫的聚集行为提供一定的参考。

关键词 昆虫; 聚集行为; 适应性策略; 聚集模式; 机制; 功能和意义

Progress in research on the aggregation behavior of insects

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Abstract Aggregation is a common phenomenon in the animal kingdom, particularly among insects. The reasons why insects aggregate are complex and varied. Most scholars attribute aggregation to environmental heterogeneity, communication, and interaction between conspecific individuals. Few studies have delved into the internal mechanism of communication and interaction, with most focusing on the transmission and recognition of chemical signals. There has been significant progress in research on insect aggregation over the past two decades. This review provides a comprehensive summary of domestic and international research on insect aggregation since the 1970's. It covers various aspects of aggregation behavior, including patterns, mechanisms, functions, significance and adaptive evolution. It is, therefore, as a valuable resource for future research on insect aggregation.

Key words insects; aggregation behavior; adaptive strategy; aggregation pattern; mechanism; function and significance

从低等动物到高等动物, 聚集行为均有发生, 主要集中在昆虫、鱼类、鸟类以及哺乳动物中。研究动物聚集行为面临环境和条件的挑战很大, 很难找到合适的研究对象, 实验操作也较为复杂, 昆虫则体现出得天独厚的优势条件。

在动物或昆虫范围内, 以聚集(Aggregation)和聚集行为(Aggregation behavior)关键词在百链数据库, 谷歌学术、百度学术、知网等平台进

行检索, 从 1963 到 2022 年, 共检索出 1 754 篇相关文献, 其中主要包括外文文献 1 600 篇, 中文文献 154 篇, 涉及聚集机制(Aggregation mechanism)关键词的文献近 40 篇, 大部分文章研究重点主要集中在化学物质对昆虫聚集行为的介导作用上。1993-2021 年期间, 动物聚集的外文文献的发表趋势相对平稳, 中文文献的发表呈逐渐增长的趋势, 昆虫聚集行为的相关研究一

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直被国内外学者所关注和重视。

昆虫聚集行为的研究有着重要的现实意义。主要体现在以下几个方面: 1. 昆虫聚集行为在生态学中扮演着重要的角色, 社会性昆虫以及非社会性昆虫能够在特定的时间和空间内聚集, 以维持整个群体的生存和发展; 2. 昆虫聚集对农林植物生长和发育也有重要影响, 许多昆虫在特定的生长阶段聚集在植物上会导致植物生长衰弱, 严重时导致植物死亡; 3. 昆虫聚集行为也对害虫防治有重要指示作用, 可以通过研究昆虫聚集行为来制定相应的防治措施; 4. 昆虫聚集行为也可以帮助研究血吸虫病、蚊媒疾病等传染病的传播机制。例如通过对蚊子聚集在特定生境中的聚集行为进行研究, 可以为帮助研究蚊媒疾病传播的机理和防治措施相关研究提供理论依据。

昆虫的聚集行为的研究也极具生物学意义。聚集行为对昆虫提高繁殖率、存活率、信息交流以及抵御不良环境等有着十分重要的作用。本文拟综述昆虫聚集行为的研究现状, 重点探讨聚集行为的发生机制, 分析现存问题, 展望今后研究方向。

1 昆虫聚集定义及类型

昆虫在一定的空间和时间下, 多个个体在生物因素或非生物因素的诱导刺激下运动形成团簇组群, 这些团簇群共同行使非社会或社会群体的行为功能, 这个过程称为聚集, 该行为则被称作聚集行为。昆虫会在可用空间的一小部分出现集合 (Collection), 这种情况下可能存在轻微的族群交互 (Allee, 1927), 族群的交互和环境的作用能够导致个体形成非随机空间分布 (Eickwort, 1981; Santiago-Blay *et al.*, 2012)。环境的驱动和个体的交流互动则会使昆虫进行被动的定向选择运动或随机运动, 使得昆虫个体大量聚集在有限面积中 (章士美, 1992)。一般来说, 聚集离不开环境和个体的共同作用, 如果它们相互接近或成组成群, 相比于随机或均匀分布的一组同种生物则被认为是聚集。

聚集是昆虫或其它动物适应环境变化、趋利避害的一种适应性策略。聚集在动物中较为普

遍。不同强度的聚合中个体数量也会不同。群居的沙漠蝗 *Schistocerca gregaria* (Forsk.) 若虫可以大规模的聚集, 个体数量庞大, 从几百个到几十万只不等 (Collett *et al.*, 1998)。树蛙 *Allobates talamancae* (Cope) 在自然条件下少则 2-3 只, 多则十几只会聚集在一起 (Hopkins and Lahanas, 2011); 有些动物或昆虫聚集则会显示出相应的流动性和一致性, 如鱼群的闪速扩张, 鱼的个体成员成固定运动模式围绕一个未被占用的圈进行有组织的运动 (Parrish and Edelstein-Keshet, 1999); 一些半翅目、膜翅目等昆虫的幼虫会出现环化 (Cycloalectic) 现象, 这些昆虫的幼虫在休息或抵御天敌时会形成一个紧密的圆圈, 头部或腹部末端并列在周围, 其余的幼虫在圆圈的中心 (Vasconcellos-Neto and Jolivet, 1988; 1989), 形成防御性的聚集体 (Jolivet and Maes, 1996)。有些聚集是在一定的时间下产生, 一些昆虫则会在产卵时发生聚集 (Desurmont and Weston, 2010, 2011; Desurmont *et al.*, 2014), 也会在取食和交配时聚集 (Milne *et al.*, 2002); 时间尺度上则表现为越冬时期和越夏时期均可能发生不同程度的聚集, 如异色瓢虫 *Harmonia axyridis* (Pallas) 并非在越冬时才会发生聚集, 越夏时期亦可发生聚集 (Durieux *et al.*, 2012, 2015)。另外, 昆虫不同时期的虫态均可组织聚集, 如卵、幼虫 (若虫)、雌虫或雄虫 (表 1)。

环境资源的利用和整合以及个体间的交流和互动使得聚集类型的划分规整并有利于一些研究者判断昆虫聚集的类型 (图 1)。Allee (1931) 将聚集分为两大类: (1) 偶发性团体或联系性团体 (Accidental unions or Associations), 主要和环境异质性相关; (2) 基础聚集或社会聚集 (Essential aggregations or Societies), 主要和个体与个体之间的联系和交互相关。这一观点在多个研究中得到证实 (Bach and Carr, 1990; Kakizaki, 2001; Jeanson and Deneubourg, 2007)。Parrish 和 Hamner (1997) 将聚合进行分类划分为两个两个主要类别, (1) 非社会性聚集 (Nonsocial aggregation)。在非社会聚合中, 个体被一个特

表 1 具有聚集行为的多种昆虫统计
Table 1 Statistics of various insects with aggregation behavior

目 Order	科 Family	属 Genus	种 Species	研究对象 Object	研究主题 Topic	文献 Reference
鞘翅目 Coleoptera	象甲科 Curculionidae	水象甲属 <i>Lissorhoptrus</i>	稻水象甲 <i>Lissorhoptrus oryzophilus</i> Kuschel	幼虫 Larvae	空间分布 Spatial distribution	Mulcahy <i>et al.</i> , 2022
		甘蔗象属 <i>Metamasius</i>	椰象 <i>Metamasius spinolae</i> Gylh.	成虫 Adults	聚集信息素 Aggregation pheromone	Malo <i>et al.</i> , 2020
		球茎象属 <i>Conotrachelus</i>	蓝莓象甲 <i>Conotrachelus nenuphar</i> (Herbst)	成虫 Adults	时空动态 Spatial dynamics	Johnattan <i>et al.</i> , 2017
		花象属 <i>Anthonomus</i>	辣椒象甲 <i>Anthonomus eugeni</i> Cano	成虫 Adults	寄主植物 Host plant	Addesso <i>et al.</i> , 2011
		<i>Scyphophorus</i>	龙舌兰象甲 <i>Scyphophorus acupunctatus</i> Gyllenhal	成虫 Adults	聚集信息素 Aggregation pheromone	Ruiz-Montiel <i>et al.</i> , 2008
		甜菜象属 <i>Bothynoderes</i>	甜菜象甲 <i>Bothynoderes punctiventris</i> (Germar)	成虫 Adults	聚集引诱剂 Aggregation attractant	Tóth <i>et al.</i> , 2007
		甘蔗象属 <i>Metamasius</i>	象甲 <i>Metamasius spinolae</i> Gylh.	成虫 Adults	聚集信息素 Aggregation pheromone	Tafoya, <i>et al.</i> , 2007
		耳喙象属 <i>Otiorhynchus</i>	葡萄黑耳喙象甲 <i>Otiorhynchus sulcatus</i> (Fabricius)	成虫 Adults	寄主和同种信号 Host and conspecific signals	Van Tol <i>et al.</i> , 2004
		根颈象属 <i>Cosmopolites</i>	香蕉象甲 <i>Cosmopolites sordidus</i> (Germar)	成虫 Adults	寄主和同种信号 Host and conspecific signals	Tinzaara <i>et al.</i> , 2003
		沟眶象属 <i>Eucryptorrhynchus</i>	臭椿沟眶象 <i>Eucryptorrhynchus brandti</i> (Harold)	成虫 Adults	同种信号与环境异质性 Conspecific signals and environmental heterogeneity	Sun <i>et al.</i> , 2023
		<i>Rhinostomus</i>	须喙足刺象甲 <i>Rhinostomus barbirostris</i> (Fabricius)	成虫 Adults	聚集信息素 Aggregation attractant	Reis <i>et al.</i> , 2018
		大小蠹属 <i>Dendroctonus</i>	红脂大小蠹 <i>Dendroctonus valens</i> LeConte	成虫 Adults	聚集机制 Aggregation mechanism	Liu <i>et al.</i> , 2020
			云杉甲虫 <i>Dendroctonus rufipennis</i> Kirby	成虫 Adults	化学信号 Chemical signal	Isitt, <i>et al.</i> , 2018
			南部松小蠹 <i>Dendroctonus frontalis</i> Zimmermann	成虫 Adults	化学信息素 Semiochemicals	Sullivan and Brownie, 2021

续表 1 (Table 1 continued)

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鞘翅目 Coleoptera	象甲科 Curculionidae	海小蠹属 <i>Hylesinus</i>	欧洲白蜡小蠹 <i>Hylesinus pruinus</i> Eichhoff	成虫 Adult	化学信息素 Semiochemicals	Shepherd <i>et al.</i> , 2010
		齿小蠹属 <i>Ips</i>	混点齿小蠹 <i>Ips confuses</i> LeConte	成虫 Adults	基因调控 Gene regulatory	Fisher <i>et al.</i> , 2021
	天牛科 Cerambycidae	星天牛属 <i>Anoplophora</i>	光肩星天牛 <i>Anoplophora glabripennis</i> (Motschulsky)	成虫 Adults	化学信息素 Semiochemicals	Bobadoye <i>et al.</i> , 2019
		颈天牛属 <i>Aromia</i>	桃颈天牛 <i>Aromia bungii</i> Faldermann	成虫 Adults	化学信息素 Semiochemicals	Yasui, <i>et al.</i> , 2018
		小扁天牛属 <i>Callidiellum</i>	红翅小扁天牛 <i>Callidiellum rufipenne</i> (Motschulsky)	成虫 Adults	接触式信息素 Contact pheromones	Rutledge <i>et al.</i> , 2009
		<i>Tetraopes</i>	马力筋红天牛 <i>Tetraopes tetrophthalmus</i> (Forster)	成虫 Adults	聚集和交配定位 Aggregation and mating localization	Peter <i>et al.</i> , 2002
	瓢虫科 Coccinellidae	长足瓢虫属 <i>Hippodamia</i>	墨西哥豆瓢虫 <i>Hippodamia undecimnotata</i> (Schneider)	成虫 Adults	越冬聚集 Overwintering aggregation	Susset <i>et al.</i> , 2017
			猫斑长足瓢虫 <i>Hippodamia convergens</i> Guérin-Méneville	成虫 Adults	能量代谢 Energy metabolism	Szejner-Sigal and Williams, 2022
			多异瓢虫 <i>Hippodamia variegata</i> Goeze	成虫 Adults	越冬聚集 Overwintering aggregation	Honek <i>et al.</i> , 2007
		瓢虫属 <i>Coccinella</i>	异色瓢虫 <i>Harmonia axyridis</i> (Pallas)	成虫 Adults	聚集机制 Aggregation mechanism 碳氢化合物 Hydrocarbons 冬天聚集 Overwintering aggregation	Durieux <i>et al.</i> , 2012, 2015; Schaefer, 2003
			七星瓢虫 <i>Coccinella septempunctata</i> L.	成虫 Adults	越冬聚集 Overwintering aggregation	Honek <i>et al.</i> , 2007
			瓢虫 <i>Ceratomegilla undecimnotata</i> (Schneider)			
	金龟子科 Scarabaeidae	弧丽金龟属 <i>Popillia</i>	日本丽金龟 <i>Popillia japonica</i> Newman	成虫 Adults	生理与行为 Physiology and Behavior	Tigresos <i>et al.</i> , 2010
	金龟子科 Scarabaeidae	齿爪鳃金龟属 <i>Holotrichia</i>	黑色金龟子 <i>Holotrichia loochooana</i> <i>loochooana</i> Sawada	成虫 Adults	适应性及信息线索 Adaptability and Signal cues	Fukaya <i>et al.</i> , 2006; Yasui <i>et al.</i> , 2007

续表 1 (Table 1 continued)

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鞘翅目 Coleoptera	金龟子科 Scarabaeidae	<i>Macrodactylus</i>	蔷薇鳃角金龟 <i>Macrodactylus subspinosus</i> (Fabricius)	成虫 Adults	同种交互 Conspecific interaction	Heath <i>et al.</i> , 2002
	吉丁虫科 Buprestidae	<i>Capnodis</i>	平头木蛀虫 <i>Capnodis tenebrionis</i> (L.)	成虫 Adults	交配聚集 Mating aggregation	Bonsignore and Jones, 2014
	埋葬甲科 Silphidae	尸葬甲属 <i>Necrodes</i>	黄角尸葬甲 <i>Necrodes littoralis</i> (L.)	幼虫 Larvae	模式和机制 Modes and Mechanisms	Gruszka <i>et al.</i> , 2020
	叶甲科 Chrysomelidae	禾谷负泥虫属 <i>Oulema</i>	黑角负泥虫 <i>Oulema melanopus</i> (L.)	成虫 Adults	空间分析 Space analysis	Reay-Jones, 2012
		毛萤叶甲属 <i>Pyrrhalta</i>	莢蒾叶甲 <i>Pyrrhalta viburni</i> (Paykull)	卵 Eggs	产卵聚集 Spawn aggregation	Desurmont and Weston, 2011
				成虫 Adults	聚集功能 Aggregation function 产卵聚集 Spawn aggregation	Desurmont and Weston, 2010; Desurmont <i>et al.</i> , 2014
		<i>Acalymma</i>	黄瓜叶甲 <i>Acalymma vittatum</i> (Fabricius)	成虫 Adults	寄主响应 Host response	Gardner <i>et al.</i> , 2015
		条叶甲属 <i>Diabrotica</i>	黄瓜十一星叶甲 <i>Diabrotica undecimpunctata</i> (Mannerheim)	成虫 Adults	聚集行为特征 Aggregation behavior traits	Luna and Xue, 2009
		弗叶甲属 <i>Phratora</i>	柳弗叶甲 <i>Phratora vulgatissima</i> (L.)	成虫 Adults	影响因素 Influencing factors	Peacock <i>et al.</i> , 2001
		侧刺跳甲属 <i>Aphthona</i>	侧刺跳甲 <i>Aphthona nigricutis</i> Foudras	成虫 Adults	化学信号 Chemical signal	Tansey <i>et al.</i> , 2005
	元蓍科 Meloidae	<i>Stenoria</i>	芫菁 <i>Stenoria analis</i> (Schaum)	幼虫 Larvae	聚集的功能 Aggregation function	Vereecken and GillesMahe, 2007
	大蕈甲科 Erotylidae	窄蕈甲属 <i>Dacne</i>	二纹窄蕈甲 <i>Dacne picta</i> Crotch	成虫和幼虫 Adults and larvae	聚集的功能 Aggregation function	Sato <i>et al.</i> , 2004
鳞翅目 Lepidoptera	夜蛾科 Noctuidae	铃夜蛾属 <i>Helicoverpa</i>	美洲棉铃虫 <i>Helicoverpa zea</i> (Boddie)	成虫和幼虫 Adults and larvae	空间分布 Spatial distribution	Ferreira <i>et al.</i> , 2021
			棉铃虫 <i>Helicoverpa</i> spp.	成虫 Adults	产卵聚集 Spawn aggregation	Sequeira and Moore, 2003
	裳蛾科 Erebidae	灯蛾属 <i>Arctia</i>	虎蛾 <i>Arctia virginalis</i> Boisduval	成虫 Adults	预测运动 Predicted movement	Grof-Tisza <i>et al.</i> , 2017

续表 1 (Table 1 continued)

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鳞翅目 Lepidoptera	灰蝶科 Lycaenidae	霾灰蝶属 <i>Maculinea</i>	灰蝶 1 <i>Maculinea nausithous</i> (Bergsträsser)	成虫和幼虫 Adults and larvae	生境选择 Habitat selection	Korosi <i>et al.</i> , 2012
			灰蝶 2 <i>Maculinea teleius</i> (Bergsträsser)			
	蛱蝶科 Nymphalidae	蛱蝶属 <i>Heliconius</i>	蛱蝶 <i>Heliconius antiochus</i> (L.)	成虫 Adults	环境因素 Environmental factors	Salcedo, 2010
	小翅蛾科 Micropterigidae	<i>Micropterix</i>	小翅蛾 <i>Micropterix maschukella</i> Alphéraky	成虫 Adults	聚集特征 Aggregated features	Kozlov and Zvereva, 2006
	刺蛾科 Limacodidae	<i>Doratifera</i>	黑色蛱蛎杯蛾 <i>Doratifera casta</i> (Scott)	幼虫 Larvae	影响因素 Influencing factors	Reader and Dieter, 2003
半翅目 Hemiptera	草螟科 Crambidae	秆野螟属 <i>Ostrinia</i>	欧洲玉米螟 <i>Ostrinia nubilalis</i> (Hübner)	成虫 Adults	影响因素 Influencing factors	Showers <i>et al.</i> , 2001
	土蝽科 Cydnidae	朱土蝽属 <i>Parastrachia</i>	日本朱土蝽 <i>Parastrachia japonensis</i> (Scott)	成虫 Adults	呼吸速率 Respiration rate	Tojo <i>et al.</i> , 2005
	蝽科 Pentatomidae	茶翅蝽属 <i>Halyomorpha</i>	茶翅蝽 <i>Halyomorpha halys</i> (Stal)	成虫 Adults	聚集形成 Aggregation formation 越冬聚集 Overwintering aggregation	Toyama <i>et al.</i> , 2006; Song and Lee, 2020
	龟蝽科 Plataspidae	豆龟蝽属 <i>Megacopta</i>	龟蝽 <i>Megacopta punctatissima</i> Montandon	成虫 Adults	交配聚集 Mating aggregation	Hosokawa and Suzuki, 2000
	猎蝽科 Reduviidae	锥蝽属 <i>Triatoma</i>	骚扰锥蝽 <i>Triatoma infestans</i> Klug	若虫和成虫 Nymphs and adults	化学信号 Chemical signal	May-Concha and Lobbia, 2018
	杆长蝽科 Blissidae	土长蝽属 <i>Blissus</i>	南方杆长蝽 <i>Blissus insuhris</i> Barber	成虫和若虫 Adults and nymphs	聚集行为 Aggregation behavior	Addesso <i>et al.</i> , 2012
	盾蝽科 Scutelleridae	扁盾蝽属 <i>Eurygaster</i>	麦扁盾蝽 <i>Eurygaster integriceps</i> Puton	成虫 Adults	时空分布 Spatiotemporal distribution	Karimzadeh <i>et al.</i> , 2011
	臭虫科 Cimicidae	臭虫属 <i>Cimex</i>	温带臭虫 <i>Cimex lectularius</i> L.	成虫 Adults	化学感受 Chemosensory 聚集行为 Aggregation behavior	Olson <i>et al.</i> , 2009; Liu <i>et al.</i> , 2017
	蚜科 Aphididae	蚜虫属 <i>Aphis</i>	大豆蚜 <i>Aphis glycines</i> Matsumura	成虫 Adults	空间分布 Spatial distribution	Tran and Koch, 2017

续表 1 (Table 1 continued)

目 Order	科 Family	属 Genus	种 Species	研究对象 Object	研究主题 Topic	文献 Reference
半翅目 Hemiptera	蚜科 Aphididae	无网管蚜属 <i>Acyrtosiphon</i>	豌豆蚜虫 <i>Acyrtosiphon pisum</i> (Koch)	成虫 Adults	行为变化 Behavior change	Muratori <i>et al.</i> , 2014
		声蚜属 <i>Toxoptera</i>	褐色橘蚜 <i>Toxoptera citricida</i> (Kirkaldy)	雌虫 Females	聚集结果 Aggregated results	Michaud and Belliure, 2000
	沫蝉科 Cercopidae	长沫蝉属 <i>Philaenus</i>	长沫蝉 <i>Philaenus spumarius</i> (L.)	成虫和若虫 Adults and nymphs	收益和成本 Benefits and costs	Wise and Kieffer, 2006
		<i>Neophilaenus</i>	沫蝉 <i>Neophilaenus albipennis</i> (Fabricius)	若虫 Nymphs	聚集特征 Aggregated features	Biedermann, 2003
双翅目 Diptera	果蝇科 Drosophilidae	果蝇属 <i>Drosophila</i>	黑腹果蝇 <i>Drosophila melanogaster</i> Meigen	雄虫 Males	聚集机制 Aggregation mechanism 行为可塑性 Behavioral plasticity	Wertheim <i>et al.</i> , 2002; Churchill <i>et al.</i> , 2020
			果蝇 <i>Drosophila simulans</i> Sturtevant	卵 Eggs	产卵聚集 Spawn aggregation	Takahashi, 2007
	丽蝇科 Calliphoridae	绿蝇属 <i>Lucilia</i>	丝光绿蝇 <i>Lucilia sericata</i> (Meigen)	幼虫 Larvae	社会适应 Social adaptation	Scanvion <i>et al.</i> , 2018
蜚蠊目 Blattaria	蜚蠊科 Blattidae	小蠊属 <i>Blattella</i>	德国小蠊 <i>Blattella germanica</i> (L.)	成虫 Adults	表皮化合物 Hydrocarbons 聚集模式 Aggregation mode 接触聚集 Contact aggregation 自发聚集 Self-organize aggregation 气味识别 Smell recognition	Ame <i>et al.</i> , 2004; Jeanson, 2005; Lihoreau and Rivault, 2008; Varadinova <i>et al.</i> , 2010; Hamilton <i>et al.</i> , 2019
		大蠊属 <i>Periplaneta</i>	美洲大蠊 <i>Periplaneta americana</i> (L.)	成虫 Adults	化学信息素 Semiochemicals	Tanaka and Daimon, 2018
	姬蠊科 Phyllodromiidae	弯翅蠊属 <i>Panesthia</i>	黑褐硬蠊 <i>Panesthia angustipennis</i> (Shiraki)	成虫 Adults	功能和意义 Function and meaning	Ito and Osawa, 2017
膜翅目 Hymenoptera	条蜂科 Anthophoridae	木蜂属 <i>Xylocopa</i>	河谷木蜂 <i>Xylocopa varipuncta</i> Smith	成虫 Adults	场所识别 Shelter identification	Ostwald <i>et al.</i> , 2019
	蜜蜂科 Apidae	蜜蜂属 <i>Apis</i>	欧洲黑蜂 <i>Apis mellifera</i> L.	成虫 Adults	越冬聚集 Overwintering aggregation	Eskov and Toboev, 2011

续表 1 (Table 1 continued)

目 Order	科 Family	属 Genus	种 Species	研究对象 Object	研究主题 Topic	文献 Reference
膜翅目 Hymenoptera	蜜蜂科 Apidae	淡脉隧蜂属 <i>Lasioglossum</i>	淡脉隧蜂 <i>Lasioglossum baleicum</i> (Cockerell)	幼虫 Larvae	聚集功能 Aggregation function	Yagi and Hasegawa, 2010
	方头泥蜂科 Crabronidae	节腹泥蜂属 <i>Cerceris</i>	沙节腹泥蜂 <i>Cerceris arenaria</i> (L.)	成虫 Adults	时空变化 Spatiotemporal change	Polidori <i>et al.</i> , 2005
	蚁科 Formicidae	毛蚁属 <i>Lasius</i>	日本毛蚁 <i>Lasius japonicus Santschi</i>	成虫 Adults	影响因素 Influencing factors	Hisamoto, 2018
		切叶蚁属 <i>Atta</i>	切叶蚁 <i>Atta sexdens rubropilosa</i> Forel	成虫和幼虫 Adults and larvae	聚集行为 Aggregation behavior	Depickere <i>et al.</i> , 2008
		火蚁属 <i>Solenopsis</i>	截火蚁 <i>Solenopsis interrupta</i>			
		举腹蚁属 <i>Crematogaster</i>	棕头举腹蚁 <i>Crematogaster scutellaris</i> (Olivier)	成虫 Adults	影响因素 Influencing factors	Depickere <i>et al.</i> , 2008a, 2008b
		毛山蚁属 <i>Lasius</i>	黑褐毛山蚁 <i>Lasius niger</i> (L.)	成虫 Adults	光线索 Light cues	Depickere <i>et al.</i> , 2004
缨翅目 Thysanoptera	蓟马科 Thripidae	大蓟马属 <i>Megalurothrips</i>	豆花蓟马 <i>Megalurothrips sjostedti</i> Trybom	成虫 Adults	化学信息素 Semiochemicals	Niassy and Ekesi, 2016
		足蓟马属 <i>Pezothrips</i>	柑桔黄绿蓟马 <i>Pezothrips kellyanus</i> (Bagnall)	成虫和若虫 Adults and nymphs	聚集模式 Aggregation mode	Navarro- Campos <i>et al.</i> , 2012
		花蓟马属 <i>Frankliniella</i>	花蓟马 <i>Frankliniella schultzei</i> (Trybom)	成虫 Adults	交配聚集 Mating aggregation	Milne <i>et al.</i> , 2002
直翅目 Orthoptera	蝗科 Acrididae	沙漠蝗属 <i>Schistocerca</i>	沙漠蝗虫 <i>Schistocerca gregaria</i> (Forskall)	成虫 Adults	聚集行为 Aggregation behavior	Rogers and Cullen, 2014
		飞蝗属 <i>Locusta</i>	东亚飞蝗 <i>Locusta migratoria manilensis</i> (Meyen)	成虫 Adults	粪便挥发物 Fecal volatiles	Shi <i>et al.</i> , 2011
	螽斯科 Tettigoniidae	草螽属 <i>Conocephalus</i>	短翅草螽 <i>Conocephalus brevipennis</i> (S.H.Scudder)	雄虫 Males	声音线索 Sound cues	Guerra and Mason, 2005
啮虫目 Psocoptera	啮虫科 Psocidae	<i>Cerastipsocus</i>	啮虫 <i>Cerastipsocus sivorii</i> Kolbe	成虫 Adults	化学信号 Chemical signal	Buzatto <i>et al.</i> , 2009
蜻蜓目 Odonata	色蟌科 Calopterygidae	<i>Hetaerina</i>	豆娘 <i>Hetaerina americana</i> (Fabricius)	成虫 Adults	特征和功能 Features and Functions	Switzer and Grether, 2000

定的资源吸引, 但不进行社会互动, 当资源被消耗或消失时, 昆虫则会分散开来; (2) 社会性聚集 (Social aggregation)。这类型是通过社会互动成员之间的相互吸引而形成和维持的, 昆虫纲个

体的社会互动在直翅目、半翅目、鞘翅目等多个目中较为常见,这两种聚集类型的划分更聚焦于聚集形成的原因和机制。

根据聚集时间的长短,彩万志和庞雄飞(2001)将昆虫的群集(Aggregation)划分为两类。(1)临时性群集(Temporary aggregation),某一虫态在一段时间内群集在一起,过后则分散这类群集被称作临时性群集,如异色瓢虫 *H. axyridis*、马铃薯瓢虫 *Henosepilachna vigintioctomaculata* Motschulsky 等一些鞘翅目昆虫越冬形成的聚

集;(2)永久性群集(Permanent aggregation)。该类群集下昆虫能终生群集在一起,一般是具有社会属性的昆虫,如蚂蚁和蜜蜂等形成的组群。但以上划分的区别界限并不明显,这种划分还和聚集个体的多少和所占据的空间的大小有关。聚焦于某个特定的时段或时期,有利于研究者们追踪这些昆虫的聚集特征。但不能忽略昆虫聚集的时间和空间,也不能割裂环境或个体互动。这些类型的划分为研究昆虫聚集行为提供了理论依据和判断标准。

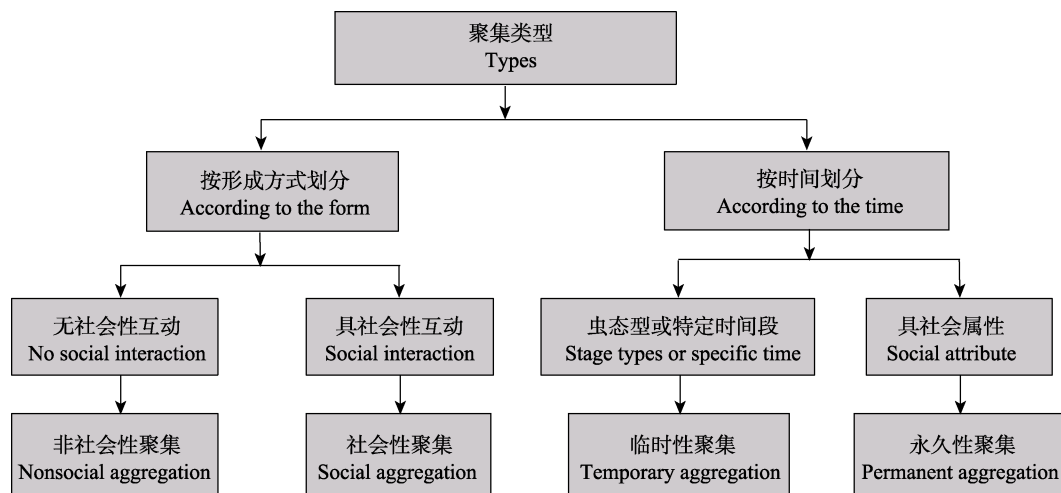


图 1 不同方式划分的聚集类型

Fig. 1 Aggregation types divided into different ways

2 昆虫聚集模式

昆虫聚集模式一般指昆虫的空间分布模式。聚集模式的形成和集体行为不仅受到环境异质性的调控而且离不开社会组分的作用。聚集时间、聚集地点、聚集形式以及是否形成种群聚集受到环境的制约(Reeve *et al.*, 1980; Gear, 2004; Gruszka *et al.*, 2020)。

对于白天活动的动物来说,夜晚是一个脆弱时期,如骚扰锥蝽 *Triatoma infestans* Klug 成虫在白天并不活跃,多在夜间发生聚集(Lorenzo Figueiras *et al.*, 1994)。夜间沙漠蝗虫 *S. gregaria* 若虫更偏向在健壮高大的植物上发生聚集,植物的异质性分布促进若虫的聚集(Despland *et al.*,

2000; Maeno *et al.*, 2018)。面临天敌的捕食或昆虫的视力障碍,为了克服这个脆弱的时期,同种动物聚集在一起寻找合适的聚集位点(Hamilton, 1982; Anderson, 1984)。在一些昆虫中如叶甲 *Pyrhalta viburni* Paykull (Desurmont and Weston, 2011) 雌性通常在产卵期时选择聚集产卵,这可能是动物或昆虫的一种适应性行为。

雄性胡蜂 *Eustenancistrocerus amadanensis* Saussure 成虫睡眠时会发生聚集(Fateryga and Fateryga, 2021)。但大多数节肢动物在成虫期形成聚集,来完成交配、取食、产卵或抵御天敌等目的,但也不乏其它形式的聚集,例如卵或幼(若)虫,这些聚集形式占据着一定的空间。这些聚集场所的选择和昆虫习性与环境异质性的交互作用密切相关,例如德国小蠊 *Blattella*

germanica (L.) 若虫在聚集位置的选择上会受到社会属性的影响, 雄性成虫会有领导作用 (Jeanson and Deneubourg, 2007)。另外, 资源在空间的集中可能会引起动物的聚集 (Collett *et al.*, 1998), 如番茄作物的一种重要害虫 B 型烟粉虱 *Bemisia tabaci* biotype B 在番茄植株和叶片上表现出高度聚集 (Rincon *et al.*, 2015)。稻红瓢虫 *Micraspis discolor* Fabricius (杜予州和陈学忠, 1993)、梨二叉蚜 *Schizaphis piricola* Matsumura (太一梅等, 2004)、栗角斑蚜 *Nippocallis kuricola* Matsumura (江宝福, 2020) 等也呈现出空间聚集分布的聚集模式。在不同分辨率或距离级别上对聚集进行研究, 每个聚集可能会产生不同的有价值的信息, 研究表明沟眶象 *E. scrobiculatus* 和臭椿沟眶象 *E. brandti* 两种象甲被证实了种群空间分布呈聚集分布, 这两种象甲的聚集的形成可能与环境异质性或昆虫本身习性相关 (杨舟斌, 2016)。同种个体交流、温度、寄主植物以及光照等因素研究会影响臭椿沟眶象 *E. brandti* 成虫的聚集 (Sun *et al.*, 2023)。

聚集模式的研究大多采用统计学上如 Talyor

幂法则法、回归检验法、聚集度指标法等方法来分析数量的变化, 只能大致通过计数指标来猜测动物形成聚集的大致原因, 但这并不能忽略其对聚集研究的基础作用和指示作用。

3 昆虫聚集行为机制

同种个体聚集在特定的地点是作为一种适应性策略, 是对不良环境所作出的相应趋利避害的响应。关于不同时空动态上聚集行为模式的出现以及聚集体内个体之间的社会互动和集体决策, 人们提出了许多不同的观点, 我们对多种昆虫的聚集行为的研究内容进行归纳、总结和讨论 (表 1)。

聚集可能是由非生物因素造成的有机体被动集合, 也可能是由于个体的积极行动而形成 (Parrish and Hamner, 1997) (图 2)。目前普遍认为昆虫聚集行为的产生和维持机制是由环境异质性和同种昆虫间的交互和信息交流共同参与驱使或介导 (Schlyter and Birgersson, 1999; Stephens and Sutherland, 1999; LioniI and Detrain, 2002)。

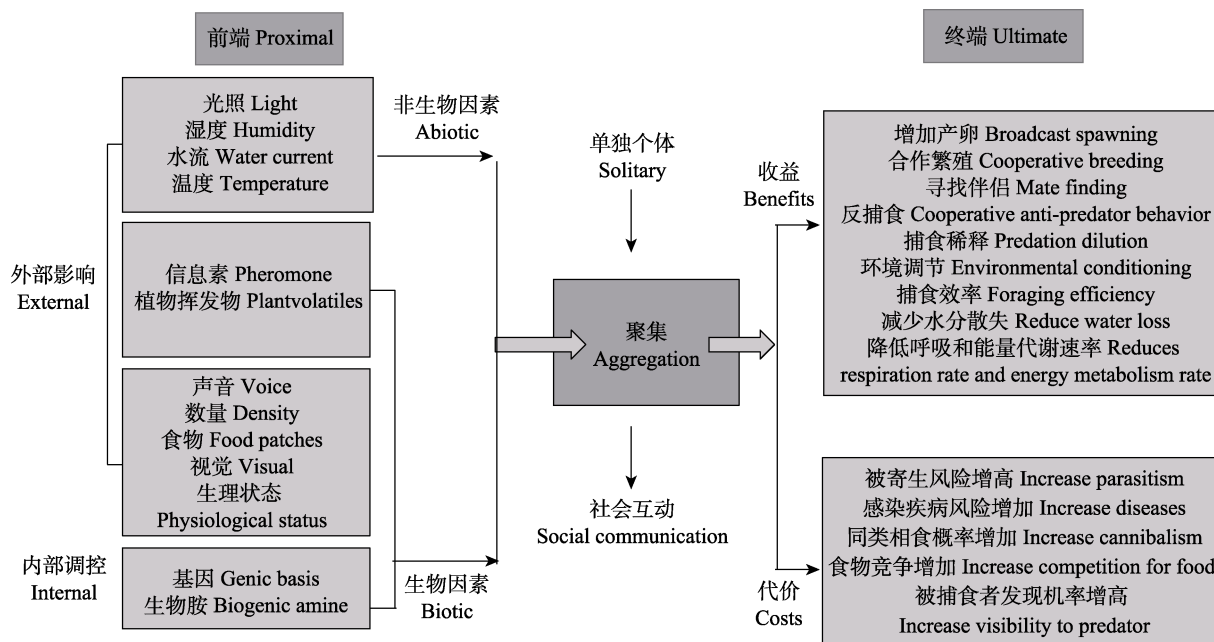


图 2 代表昆虫聚集行为的一些终端结果 (收益和代价) 和前端原因 (生物和非生物因素) 的概念和综合模式 (仿 Broly *et al.*, 2013)

Fig. 2 Concepts and integrated models represent some ends results (benefits and costs) and proximal causes (biotic and abiotic factors) of aggregation behavior of insects (motified from Broly *et al.*, 2013)

3.1 环境异质性驱动的昆虫聚集

环境异质性驱动着聚集行为。主要包括一些非生物因素如光照强度、湿度、温度、空气流速、水流压力、潮汐等在动物的行为研究中占据相对重要地位。聚集并不是固定模式，而是一种根据地点、季节、动物的成熟度和基质而变化的策略，使得有利于适应不同基质和环境条件 (Fischer *et al.*, 2012)。昆虫作为环境的作用主体，如趋温性、趋光性、趋暗性以及趋湿性等昆虫趋性能对环境的不同非生物因素做出响应。斑衣鱼 *Thermobia domestica* (Packard) 对温度表现出偏好反应，相对于 20 °C 的室温环境，偏爱 35 °C 的高温环境，同时黑色栖息地比白色居住场所更有吸引力 (Tremblay and Gries, 2006)；多数昆虫存在趋光行为，由于昆虫复眼结构和一些光敏色素的特征，不同种类的昆虫对光能表现出相应的选择和偏好 (Shimizu and Kato, 1978)，如梨小食心虫 *Grapholita molesta* Busck 和草地螟 *Loxostege sticticalis* (L.) 等。昆虫的视觉信号通讯在昆虫与植物之间也发挥着重要的作用 (文超等, 2019)，如茶二叉蚜 *Toxoptera aurantia* (Boyer) 对素馨黄和芽绿色的趋向性最强，具有显著的趋黄和趋绿性 (崔林等, 2014)。

3.2 种内通讯驱动的昆虫聚集

同种个体的交流互动引起昆虫或动物聚集行为。在这个过程中主要包括一些化学信号和物理信号的传递。昆虫嗅觉、视觉、听觉、触觉等在昆虫信息交流过程中起到重要作用。

触角是化学信息素的主要感受器官。一些昆虫的个体之间的交流主要依靠化学信息素的介导和维持，它们主动寻找彼此，并在特定时期形成聚集 (Wertheim *et al.*, 2005)。随着化学生态学的发展和分析技术的进步，多种鳞翅目昆虫的化学信息素被分离鉴定出来，苹果蠹蛾 *Cydia pomonella* L. 幼虫对合成的 (E)-2-辛烯醛 ((E)-2-Octenal)、(E)-2-壬烯醛 ((E)-2-Nonenal)、磺卡酮 (Sulcatone) 和香叶酮 (Geranylacetone) 与 3-葑烯 (3-carene) 和/或 3 种饱和醛 (辛醛

(Octanal)、壬醛 (Nonanal)、癸醛 (Decanal)) 结合的混合物有强烈反应，这几种成分可能是幼虫的聚集信息素 (Jumeau *et al.*, 2005)；大豆夜蛾 *Anticarsia gemmatilis* Hubner 雄性产生的信息素 3,6,9-二十一碳三烯 ((Z,Z,Z)-3,6,9-heneicosatriene) 对雄性有强烈的吸引效果 (Heath *et al.*, 1998) 等。直翅目代表昆虫亚洲飞蝗 *Locusta migratoria* (L.) 被通过分析体表以及粪便挥发物，在 35 种化合物中鉴定到了一种由群居型蝗虫特异性挥发的气味，释放量低但生物活性非常高的化合物 4-乙基苯甲醚 (4-vinylanisole)，随后从化学分析，行为验证，神经电生理记录，嗅觉受体鉴定，基因敲除，野外验证等多个层面对飞蝗群居信息素进行了全面而充分的鉴定和验证，发现和确立了 4-乙基苯甲醚是飞蝗的聚集信息素，这种微量且生物活性高的物质介导着飞蝗的聚集行为 (Guo *et al.*, 2020)。聚集信息素在鞘翅目昆虫的聚集中发挥着重要的作用，已经鉴定出许多鞘翅目昆虫的聚集信息素，如华山松木蠹象 *Pissodes punctatus* Langoret (泽桑梓等, 2010) 及多种象甲科昆虫 (靳秀芳, 2019; Bandeira *et al.*, 2021)、脐腹小蠹 *Scolytus schevyrewi* Semenov (范丽华等, 2015)、华北大黑鳃金龟 *Holotrichia oblita* Faldermann (李雪等, 2018)、西花蓟马 *Frankliniella occidentalis* (Pergande) (孙冉冉等, 2020) 等，这些被鉴定出来的化学信息素在害虫的监测和防治上均得到有效利用。

物理信号如视觉、听觉以及触觉等也可起到信号交流的作用，从而促成聚集 (Bradbury and Vehrencamp, 1998)。德国小蠹 *B. germanica* 能感知其它个体体躯相互接触的刺激 (Izutsu *et al.*, 1970)，当德国小蠹若虫受到触觉刺激时比孤立的若虫生长得快 (Lihoreau and Rivault, 2008)。在非社会性聚集类型中，如柑橘木虱 *Diaphorina citri* Kuwayama (Mankin *et al.*, 2020)，西松甲虫 *Dendroctonus brevicomis* LeConte (Pureswaran *et al.*, 2016)，树皮甲虫 *Hylurgus ligniperda* (Fabricius) (Bedoya *et al.*, 2019) 等昆虫依靠一些声学信号来传递信号，声音聚集信

号的吸引力和特征在种群交流聚集过程中起到重要作用 (Takács *et al.*, 2003)。

个体数量也是影响昆虫聚集的原因之一。个体数量的增多可能会增大种内通讯交流的机率。群居的沙漠蝗若虫强烈地聚集, 个体数量庞大, 从几百个到近 50 万只不等 (Collett *et al.*, 1998), 一定种群密度下群居蝗虫个体相互吸引并进行远距离迁移。在异色瓢虫 *H. axyridis* 也发现了相似的结果, 个体数量越多, 聚集越强烈 (Durieux *et al.*, 2015)。

昆虫的生理状态或者健康程度和聚集有直接联系, 生理状态良好的个体更有利于参与种内互动。积极参与交配行为的雄性的生理状况相对较好时将会选择相对优质 (如产卵较多) 的雌性 (Parker, 1983; Bonduriansky, 2001)。日本甲虫 *Popillia japonica* (Newman) 的交配和聚集行为依赖于雄性的生理状态和雌性的繁殖状况 (Tigreros *et al.*, 2010), 配对的雄性日本甲虫有最高的脂质水平, 而未配对的孤立的雄性脂质水平最低, 在交配频率较高的时候被捕获的雌虫比在交配频率较低的时候被捕获的雌虫产卵量高。

3.3 寄主植物诱发的昆虫聚集

寄主植物是昆虫最重要的资源之一, 当竞争对手和同种个体聚集在一起获取资源时, 寄主植物资源的集聚会增加他们的相遇概率 (Emlen and Oring, 1977)。资源异质导致昆虫的聚集及其行为上的变化并不是要讨论的重点, 主要关注昆虫对寄主植物的气味感知从而引发昆虫的群体聚集。

对于一些植食性昆虫来说, 植食性昆虫依赖于寄主植物释放的挥发物感知寄主植物挥发物而取食、定位以及繁殖等。芦笋叶甲 *Crioceris duodecimpunctata* (Linnaeus) 雌雄虫对其寄主植物挥发物 1-己烯-3-醇 ((Z)-3-hexen-1-ol) 表现出最强触角电位反应和明显的趋向行为反应 (Pistillo *et al.*, 2022)。臭椿树的不同部位的离体挥发物对沟眶象 *E. scrobiculatus* 和臭椿沟眶象 *E. brandti* 有明显的吸引力 (Wen *et al.*, 2021)。寄主植物挥发物可能是单种或者多种物质共同吸引昆虫, 多数情况下多种物质的吸引力

要更强 (Wei and Kang, 2006)。在两个倍半萜烯 α -姜烯 (α -Zingiberene) 和双环大牻牛儿烯 (Bicyclogermacrene) 的共同作用下, 捕食性蝽 *Perillus bioculatus* (Fabricius) 对马铃薯甲虫 *Leptinotarsa decemlineata* Say 危害的马铃薯有着明显的趋性 (Weissbecker *et al.*, 2000)。另外, 寄主植物的挥发物和化学信息素的协同作用能增强对植食性昆虫的吸引力, 来达到相应的诱集效果。Reis 等 (2018) 在合成的须喙足刺象甲 *Rhinostomus barbirostris* (Fabricius) 的聚集信息素 (4S,5R)-isomer 中加入寄主植物挥发物粗提物对象甲的吸引力强于只有聚集信息素对象甲的吸引力。

3.4 遗传因子调控昆虫聚集

遗传因子来调控聚集行为的多数研究主要集中在嗅觉识别气味的基因调控上。昆虫受益于化学感觉神经系统的进化, 这种神经系统能够感知化学信号并处理它们的编码信息。昆虫的嗅觉识别过程始于外周嗅觉系统有选择地检测气味物质, 气味分子通过搭载水溶性气味结合蛋白 (Odorant-binding proteins, OBPs) 形成配体运送至嗅觉受体神经元 (Olfactory receptor neurons, ORNs), 随后与嗅觉受体 (Olfactory receptor, ORs) 特异性结合, 将化学信号转换为电信号后向嗅觉中枢传递, 激活了整个嗅觉信号的转导过程, 从而起到介导昆虫行为的作用 (Krieger and Breer, 2003)。许多昆虫的 OBP 和 OR 基因得到鉴定, 在化学信号的传导过程中 OBPs 和 ORs 至关重要。昆虫 OBPs 蛋白通常由 135-220 个氨基酸组成, 不同昆虫种间序列相似性较低, 但典型 OBPs 结构中均存在 6 个保守的半胱氨酸位点 (Krieger and Breer, 1999)。不同物种的 ORs 数量存在很大的差异, 一些蚂蚁和蜜蜂的 OR 数量较高 (Robertson *et al.*, 2010; Zhou *et al.*, 2015; McKenzie and Kronauer, 2018)。实时荧光定量 PCR 法是检测分析 OR 基因表达最常用最有效的方法。昆虫触角是大多数昆虫的组织表达特征家蚕 *Bombyx mori* (L.) BmorOBPs (Krieger *et al.*, 1999、亚洲玉米螟 *Ostrinia furnacalis* (Guenée) 的 OfurPBP3 (Allen and Wanner, 2011)、棉铃虫

Helicoverpa armigera (Hübner) 的 HarmPBPs (Guo *et al.*, 2012) 和 HarmOBP2 (Wang *et al.*, 2003), 但也不乏在如腹部、头部以及翅等昆虫其它部位表达 (Vogel *et al.*, 2010; Hua *et al.*, 2012)。

OR 基因的表达承载着该类基因相应的功能, RNA 干扰一般是被用来阐明该类基因功能的技术手段。特异性 ORs 负责检测昆虫信息素这类配体常被称为信息素受体 PRs。多数 PRs 的序列相似性较高, 这也成为筛选蛾类 PR 基因的关键依据 (Zhang and Christer, 2015)。除了蛾类昆虫外, 像黑腹果蝇 *Drosophila melanogaster* Meigen (Ejima *et al.*, 2007)、西方蜜蜂 *Apis mellifera* L. (Wanner *et al.*, 2007)、温带臭虫 *Cimex lectularius* Linnaeus (Liu *et al.*, 2017)、胡桃楸虎天牛 *Megacyllene caryae* (Gahan) (Mitchell *et al.*, 2012) 等昆虫的特异性 ORs 也能识别相应的性信息素和聚集信息素成分。普通 ORs 负责监测环境中的相关气味, 植物挥发物配体则常被研究, 进一步了解不同物种间的信息交流。

4 昆虫聚集行为的功能和意义

4.1 昆虫聚集行为的益处

聚集有利于昆虫繁殖。德国小蠊 *B. germanica* 和美洲大蠊 *Periplaneta americana* (Linnaeus) 隔离会降低若虫的发育率和卵囊的产生率 (Roth and Willis, 2014), 从而导致蟑螂的繁殖率降低。

聚集能够促进昆虫个体的存活和生长。云杉树皮甲虫 *Dendroctonus micans* (Kugelann) 的卵的大小和幼虫的生长之间呈正相关关系, 这种结果的产生和减弱树皮的防御有关 (Storer *et al.*, 1997)。

聚集有利于昆虫防御天敌, 无论被捕食者是警示还是隐蔽, 群居生活的一个普遍好处是可以降低天敌的捕获率, 稀释被捕获的风险 (Vulinec, 1990; Hotová Svádová, 2014)。暴露在捕食者面前的蚜虫 *Aphis varians* Patch 种群增长率随着蚜虫群大小的增加而增加, 但在未受捕食者侵害的群落中, 种群增长率总体较高 (Turchin and Kareiva, 1989), 蚜虫所在群体的大小增加, 被

瓢虫捕食的单个个体的平均风险降低。像绿蝽 *Nezara viridula* (L.) 的 1-3 龄若虫形成聚集比单个若虫更能有效地击退天敌 (Lockwood and Story, 1985); 密集聚集的灰松蚜虫 *Schizolachnus pineti* (F.) 幼虫摆动的腹部和伸展的后足似乎向临近个体传达一个告警信息, 以免受天敌的攻击 (Kidd, 1982)。

聚集有利于昆虫减少水分散失以及降低呼吸速率和代谢速率。环境对聚集群体在一定程度上是有利的, 较高的温度有利于若虫和幼虫的生长, 较高的相对湿度可能会减少聚集个体的失水 (Wertheim *et al.*, 2005), 但聚集群体在面对不利环境如极端天气时, 聚集的个体可通过降低自身的呼吸速率和能量代谢速率应对这些不利环境。滞育期间日本朱土蝽 *Parastrachia japonensis* (Scott) 聚集群体有助于代谢速率的降低 (Tojo *et al.*, 2005); 木虱个体为了防止水分的流失则会形成聚集 (Paris, 1963)。异色瓢虫 *H. axyridis* 和始红蝽 *Pyrrhocoris apterus* (L.) 随着聚集虫数的增加, 呼吸速率和能量代谢速率均降低, 从而有利用种群越冬 (苏延乐等, 2008; 赵静等, 2014)。这表明聚集行为可以减少水分流失以及降低个体的呼吸速率和能量代谢速率。

4.2 昆虫聚集行为的代价

聚集行为也带来了一定的风险。聚集行为可能会使得资源变得匮乏, 如单独的黑褐硬蠊 *Panesthia angustipennis spadica* (Shiraki) 若虫比聚集若虫生长更快、更大, 捕食和环境条件, 可能驱动了蟑螂的聚集行为 (Ito and Osawa, 2017)。

聚集比单独的个体更容易被发现, 一旦捕食者发现猎物, 它可能会耗尽整个群体 (Alatalo and Mappes, 1996; Tullberg *et al.*, 2000; Beatty *et al.*, 2005)。黑腹果蝇 *D. melanogaster* 的聚集信息素使得寄生蜂 *Leptopilina heterotoma* (Thomson) 对黑腹果蝇幼虫反应更加明显, 聚集信息素剂量的增加会吸引更多的寄生蜂, 从而增大了黑腹果蝇被寄生的概率 (Wertheim *et al.*, 2003)。

聚集导致昆虫个体之间的竞争更加激烈。在极度拥挤的条件下, 高密度减缓了美洲大蠊 *P. americana* 若虫的生长速度并增加了其死亡率

(Wharton and Wharton, 1965); Wileyto 和 Boush (1983) 对蟑螂的群体和个体进行饲养, 发现随着群体规模的增加, 成活率和生长率存在降低的可能。这可能是由于资源的分布不均, 组群内的个体会争抢更多的有利资源, 导致组群的个体间的竞争加剧, 从而导致生长率和成活率的下降。

聚集导致昆虫所在的局部环境恶化。随着植食性昆虫聚集虫数的增多, 植物的防御也会越来越强烈 (Gilbert *et al.*, 2001), 导致多数植物在防御过程中一些化学成分的含量升高。当昆虫聚集的卵团的大小一旦增加到某个临界点, 卵团中心的卵可能会经历缺氧, 卵的孵化则无法顺利完成 (Imhof and Smith, 1979)。

聚集可能增加昆虫被病菌侵染的风险。在群居物种中, 传染病的传播和维持取决于群体内个体之间的接触模式和群体之间的相互作用, 群居可能会增加被病原体感染的可能性 (Naug and Camazine, 2002)。但骚扰锥蝽 *T. infestans* 可以将粪便沉积在它们共同的住所外, 稀释了被病菌侵染的风险和降低了被寄生的概率 (Lorenzo and Lazzari, 1996)。

5 潜在的适应性进化

高于个体水平的进化意味着群体会形成一套超出了个体成员所展示的行为。如果这种联系赋予群体成员平均健康或生殖优势, 这种优势就会比它们作为个体生活在同一群体之外的优势更明显, 那么群体更有可能形成和维持。社会行为 (群体的形成和维持) 和个体行为在内的行为遗传基础研究是进化生物学研究的重点方向 (Santiago-Blay *et al.*, 2012)。个体之间存在基因上的联系, 即使这个群体中的存在某些个体的不良反应, 但这个基因相关群体的整体适合度就会增强, 相关行为可能会保持下去 (Mitaka *et al.*, 2020)。如在嗅觉受体基因中, 许多膜翅目昆虫 (蜜蜂、蚂蚁) 出现了嗅觉受体基因扩增现象, 这种现象说明了群居昆虫对环境有一种适应性进化 (Yan *et al.*, 2020)。

昆虫的群体策略是对相应环境的利弊权衡。较大群体可能拥有更大的可见性或对天敌的暴

露程度相平衡的群体优势 (如化学保护或警示性保护) (Santiago-Blay *et al.*, 2012)。雌性蛱蝶 *Hypolimnas anomala* Wallace 积极地保护它们的卵和一龄幼虫以抵御掠食性蚂蚁的侵袭, 通过拍打翅膀或者将翅覆盖在卵上来提高了卵和一龄幼虫的存活率 (Schreiner and Nafus, 2010), 这种亲代保护可能有利于亚社会性的进化发展。亲代为何会出现保护子代, 栖息环境、资源稀少、捕食者水平等多种因素被考虑在内 (Wilson, 1975), 这可能与群体的死亡率如何随群体规模而变化有关。

6 总结与展望

目前生态学、分子学、基因组学和生理学等方法已经应用到行为学的研究中。这些研究方法和手段的应用试图描绘调控行为途径的整个脉络。聚集行为是昆虫重要的防御和保护行为, 能够应对不良环境, 趋利避害。这种行为和昆虫的生存密切相关, 昆虫的聚集与环境、行为习性和信息交流密不可分。

环境异质性和同种社会交互是驱动昆虫聚集行为的产生的主要因素。环境中的资源分布如植物资源块的分布, 以及微环境的环境条件如光照、温度、湿度等因子也影响昆虫的偏好性, 主要表现在昆虫对于栖息地位置的选择、取食和交配聚集等相关行为上。昆虫源和植物源化学信号、昆虫的视觉信号、触觉信号和声音信号等在昆虫社会互动和聚集过程中发挥着重要作用, 这些信号的接收和传递促成昆虫聚集。目前, 大多数研究重点关注化学信息物质对昆虫聚集行为的介导作用, 这些化学信息物质微量、高效且具有特异性, 这种化学信号对聚集行为的作用可能最为重要, 但对于其他信号的研究也不应忽视。研究者更应该全面的、系统的进行相关研究对象的聚集行为研究, 更充分的将聚集这一行为研究透彻。

行为神经科学的一个核心目标是了解基因如何编码行为以及环境因素如何影响这些相关基因的表达, 以及内在激素的产生和调控。多种昆虫的 OR 基因得以鉴定, 不同物种之间数量上

有很大差异。ORs 数量的多样性可能和不同物种的生态学特性有关 (Mitchell *et al.*, 2020)。内在激素如何调控昆虫聚集行为的研究较少, 这可能和昆虫的物种有关, 表型上的可塑性 (如沙漠蝗虫的群居型和独居型) 可能更凸显内在激素的作用。内在激素生物胺是调控行为发生转变的关键角色。茶酚胺多巴胺 (DA) 和章鱼胺 (OA) 和 5-羟色胺 (5-HT) 调节着昆虫如进食、睡眠和清醒、学习和记忆、觉醒和攻击等多种行为 (Byrne and Certel, 2019)。在亚洲飞蝗 *L. migratoria* 中被充分证明多巴胺及其合成过程的关键基因是调控飞蝗聚集行为的重要机制, 多巴胺通路控制着飞蝗聚集行为的转变 (Chen *et al.*, 2022)。生物胺的研究对不同行为的调控也为研究神经激素对聚集行为的调控打开一个全新的方向。

当然, 在研究过程中也会存在一些问题。聚集行为的产生和维持是一个动态的过程, 但大多数的研究以静态的特征如聚集数量和聚集群体数量的变化来进行描述。另外, 环境因素对聚集行为产生的驱动上只局限于一些因素的变化和影响上, 大部分的研究并未结合生态的综合作用来进行考量。对此, 可以利用景观生态中的方法在不同尺度下来研究环境因素和昆虫群体数量上的相关性以及寄主的联通对昆虫聚集过程的影响。

聚集行为的功能和意义表明昆虫在聚集过程中存在对环境的适应, 这为研究其适应性进化提供了有利条件。对于产生聚集的信号个体 (发送者) 和对信号作出反应的个体 (接收者), 聚集可能有不同的适合度效应 (Fitness effects)。同种密度的积极影响体现在瓢虫对蚜虫的稀释效应 (Turchin and Kareiva, 1989), 以及成虫密度的增加对黑腹果蝇幼虫的积极影响 (Wertheim, 2002) 上。聚集适合度是未来研究的一个重要方向, 需要扩展到更广泛的物种和包括情况的选择上来研究聚集的益处和代价, 来获取更多的数据。

内在机理的探究将是未来研究中的主要方向, 涉及分子生物学、生理生化、以及行为神经学多个层面。Bono 和 Bargmann (1998) 利用群居的野生线虫和独居的野生线虫之间的觅食差异, 分析了单株 N2 中产生 EMS 诱导突变, 单

个氨基酸在神经肽受体 *npr-1* 中变化, 从而导致聚集行为的产生。接下来的研究中发现 3 个 QTLs 受体影响聚集行为, 其中一个 QTL, 位于 GABA 神经递质受体基因 *exp-1* 附近, 而这个特殊的受体基因和 GABA 是调控聚集的重要参与者 (Bendesky *et al.*, 2012)。近几年来, 基于遗传的工具和操作的技术的提高正在将行为领域的研究不断向前推进, 利用无脊椎动物来研究调节社会行为的遗传和生理机制, 有利于阐明了昆虫行为与神经系统的内在机制, 这对研究聚集行为意义重大。

外在原因主要是探讨聚集行为的诱发因素, 这些因素的探讨和研究有助于我们对害虫的综合防治和管理。现实地考虑聚集行为研究的实际意义, 包括害虫的综合治理以及调控昆虫-植物间的关系, 关于聚集行为的各个观点的碰撞提供了对昆虫聚集研究的不同方向以及相应的理论基础和实际指导。从昆虫聚集行为出发, 充分利用聚集进行害虫治理, 当对害虫无趋避效果的杀虫剂被昆虫接触或进食后在昆虫聚集过程中传递到其他同种个体上发生水平转移, 进而侵染同种个体, 像台湾乳白蚁 *Coptotermes formosanus* Shiraki (Bhatta and Henderson, 2016)、温带臭虫 *C. lectularius* (Akhtar and Isman, 2013)、黄野螟 *Heortia vitessoides* (Moore) (Qian *et al.*, 2023) 等具有聚集性的昆虫被合适、缓效且无趋避性的杀虫剂侵染后可进行有效防控。通过人为改变昆虫的生存环境, 使得这些害虫在迁徙或扩散的过程中无法形成规模性聚集体, 在移除林间杂草后沟眶象 *E. scrobiculatus* 数量明显降低, 这种方法能够有效降低沟眶象成虫的种群密度 (Yang and Wen, 2022), 大大降低昆虫对植物的危害。另外, 化学信息素在“推-拉” (“Push-Pull”) 策略上的应用和一些利用昆虫趋性等物理防治措施的技术手段, 降低了林间害虫的种群密度, 使之处于经济阈值之下。

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