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COMPREHENSIVE REVIEW

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Regulatory mechanisms of reproduction in locusts and grasshoppers

Jing He[1] | Jiliang Wang[1,2] | Xinran Wang[1,2]

[1]State Key Laboratory of Animal Biodiversity Conservation and Integrated Pest Management, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

[2]University of Chinese Academy of Sciences, Beijing, China

Correspondence

Jing He.
Email: hejing@ioz.ac.cn

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Abstract

Locusts and grasshoppers are worldwide agricultural pests, with their reproductive regulation serving as the critical basis for group growth and dispersal. Advances in bioinformatics and molecular biology have expanded the understanding of reproductive regulation beyond physiological responses and classical neural control. Numerous coding and noncoding genes participate in the intricate regulatory networks of reproduction. Studies on locusts and grasshoppers not only shed light on regulatory mechanisms of non-*Drosophila* insects but also identify potential targets for pest control. However, a comprehensive summary of reproductive regulatory mechanisms in locusts and grasshoppers remains lacking. Here, we synthesize key findings on hormones, neuropeptides and neurotransmitters, multifunctional integrative genes, epigenetic factors, and population density-dependent regulation. We strengthen the interplay between extrinsic environmental factors and intrinsic gonadal systems of locusts and grasshoppers. Finally, we propose future directions for studies on the regulation of reproduction in locusts and grasshoppers.

KEYWORDS

environmental signal, gonad development, phenotypic plasticity, reproduction

1 | INTRODUCTION

Grasshoppers belong to the order Orthoptera and the superfamily Acridoidea, with locusts representing the species that exhibit swarming characteristics. Both locusts and nonswarming grasshoppers are notorious agricultural pests in the world.[1] Long-term accumulation of eggs is critical for population growth; thus, reproductive capacity serves as the fundamental prerequisite for pest outbreaks. Locusts and grasshoppers apply multiple strategies to ensure reproductive success. On one hand, females lay eggs in an egg pod containing a cluster of eggs, which is covered by a mixture of their secretions and soil. This structure helps the eggs retain moisture and evade predators and parasitoids.[2] Additionally, synchronous hatching within egg pods enables the short-term formation of locust nymph aggregations.[3,4] On the other hand, the locust exhibits typical phenotypic plasticity in response to population density changes. High-density gregarious locusts and low-density solitarious locusts adopt distinct reproductive strategies to sustain population growth,[5] making them distinct models for studying density-regulated reproductive plasticity. Therefore, controlling the fecundity of locusts and grasshoppers serves as a key tactic in integrated pest management (IPM).

Studies on the regulatory factors underlying the reproductive processes of locusts and grasshoppers hold substantial significance. Firstly, gaining a comprehensive understanding of the reproductive regulatory

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mechanisms offers valuable insights into the implementation of IPM strategies. Early studies established foundational knowledge of the anatomical structure and the basic physiological activity of the reproductive system.[1] The development of neurobiology, genomics, and molecular biology enables deeper insights into the intricate regulatory networks in gonad development, mating behavior, oviposition, and egg hatching. Researchers identified multiple coding and noncoding genes involved in reproductive regulation, providing potential targets for eco-friendly pest control strategies. Moreover, recent advances highlight the integrative regulation of external environmental cues, neural signaling, and the reproductive system, positioning locusts and grasshoppers as key non-*Drosophila* models for studying insect reproduction. For instance, the fecundity plasticity and transgenerational effects of locusts in response to population density demonstrate an optimal reproductive strategy for environmental adaptation. Additionally, locusts and grasshoppers serve as ideal models for studying vitellogenesis mechanisms, which differ from those of *Drosophila*. In the context of typical panoistic ovaries, vitellogenin (Vg) is synthesized as a precursor in the fat body, secreted into the hemolymph, processed into mature forms, and then taken up by oocytes via Vg receptor (VgR)-mediated endocytosis.[6] Owing to the indispensable role in egg production, this vitellogenesis process garnered substantial research attention and has been systematically elaborated in a prior review.[7] Nevertheless, we focus on diverse regulatory factors such as neuropeptides, hormones, and environmental cues that act on the vitellogenesis process in this paper.

Although the canonical regulatory pathways, such as hormone-mediated ovarian development as well as neuropeptide- or neurotransmitter-controlled reproductive physiology in insects, have been previously discussed in separate reviews,[8,9] recent studies provide novel insights into both classical and noncanonical regulators in reproductive control. However, a comprehensive synthesis of the regulatory mechanisms in the reproduction of locusts and grasshoppers remains lacking. Here, we consolidate the progress on reproductive regulation in locusts and grasshoppers, including hormones, neuropeptides and neurotransmitters, multifunctional integrative genes, epigenetic factors, and population density effects. Although major progress has been derived from studies on the migratory locust, *Locusta migratoria*, and the desert locust, *Schistocerca gregaria*, we also incorporate findings from other species in this review. We emphasize the roles of diverse modulation pathways in mediating crosstalk between environmental signals and reproductive functions. Furthermore, we discuss the application prospects of the reproduction regulators in pest control and also raise the unresolved questions in studies of locust and grasshopper reproduction.

2 | CODING GENE REGULATION ON REPRODUCTION

2.1 | Hormones

The two canonical hormones, juvenile hormone (JH) and ecdysteroid 20-hydroxyecdysone (20E), are extensively studied regulators of insect reproduction. JH is synthesized in the corpora allata (CA), whereas 20E is produced in multiple tissues of adult insects. Notably, JH can induce vitellogenesis independently of 20E in locusts, a regulatory manner different from other insects. 20E mainly functions in ovulation and oviposition.[6,8] Although the roles of JH and 20E in female insect reproduction have been thoroughly reviewed,[8] this section focuses on recent advances since 2024 in hormone-mediated reproductive regulation in locusts, as well as the functions of JH and 20E in male reproduction.

JH regulates multiple aspects of vitellogenesis in locusts and grasshoppers, including *Vg* expression in the fat body, Vg protein (yolk protein) transportation via the hemolymph, and the uptake of Vg into developing oocytes.[6] Recent studies have unveiled networks between JH and other signaling pathways in reproductive regulation. JH and nutrient signals collaboratively regulate the transcription factor CREBB, which, in turn, activates *PGC-1α* transcription, leading to mitochondrial biogenesis and fat body remodeling. Consequently, the fat body undergoes a transformation from an energy reserve in larvae to a Vg synthesis center in adults.[10] Furthermore, JH–bone morphogenetic protein (BMP) interactions regulate the fat body transition from the previtellogenic to the vitellogenic stage. BMP signaling induces cell proliferation in the previtellogenic stage, whereas JH inhibits cell proliferation at the vitellogenic stage through the fizzy-related protein (Fzr)-mediated ubiquitination of BMP pathway proteins.[10] Additionally, JH and insulin-like peptides collaboratively enhance the phosphorylation of extracellular signal-regulated kinase, thereby stimulating *Vg* expression in the fat body.[11] In turn, JH-induced massive synthesis of Vg and oocyte growth lead to a reduction in the flight performance of females at the vitellogenic stage, due to a reproduction-flight trade-off.[12]

Although less understood than in females, JH and 20E may regulate male reproduction through the male accessory gland (MAG), a tissue that secretes bioactive molecules aiding in sperm storage and fertilization.[13] The two hormones influence protein/RNA synthesis in MAG tubules in a dose- and region-dependent manner.[14,15] Additionally, in the grasshopper *Melanoplus sanguinipes*, these two hormones exert opposite effects on most protein synthesis.[16] Knocking down the 20E receptors, ecdysone receptor (EcR) and retinoid-X receptor, delays male mating behavior without affecting fertility. Unexpectedly, RNA interference (RNAi) of EcR

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increases the mass of MAG.[17] However, the intricate regulatory pathway of hormone/receptor-regulated male reproduction remains unclear.

Collectively, the studies underscore the critical role of hormonal regulation in female locust reproduction. Future research is needed to elucidate the functions of JH, 20E, and other hormones in male reproduction.

2.2 | Neuropeptides and neurotransmitters

Neuropeptides and neurotransmitters are widely involved in diverse physiological processes of locusts and grasshoppers, including flight,[18] feeding,[19] body color,[20] and behavioral plasticity.[21] Numbers of studies revealed the regulatory roles of neuropeptides and neurotransmitters across multiple reproductive processes, from reproductive tissue development and mating behaviors to genital tract contractions.

2.2.1 | Neuropeptides and neurotransmitters regulate reproductive tissue development

Neurohemal lobes of corpora cardiaca (NCC)-derived neuropeptides that regulate insect gonad maturation are termed gonadotropins, including parsins (pacifastins, neuroparsins (NPs), ovary maturating parsins, and insulin-related peptides) and other neuropeptides. Although the sequence characteristics and functions of insect gonadotropins were previously reviewed,[22] recent studies highlight the functions of additional neuropeptides such as adipokinetic hormone III and adipokinetic hormone/corazonin-related peptide (ACP) in locust germline development (Table 1). Notably, although most neuropeptides promote reproductive development, NPs and ACP inhibit locust reproduction. NPs repress the development of the ovary and MAG, probably due to the antijuvenile hormone and antidiuretic effects of NPs,[24–26] whereas ACP reduces locust fecundity, possibly by regulating fat body lipid metabolism[29] (Table 1).

Unlike neuropeptides, the role of neurotransmitters in locust gonad development remains unclear.

2.2.2 | Neuropeptides and neurotransmitters regulate the mating behaviors

Neuropeptide- and neurotransmitter-regulated mating behaviors are primarily investigated in the grasshopper *Chorthippus biguttulus*, which serves as a model for studying acoustically driven sexual interactions. Species-specific calling songs facilitate mate recognition for both males and females.[30] Particularly, females exhibit high response thresholds to male songs, placing greater weight on nonattractive syllables than on attractive ones to avoid costly mismatches.[31] The songs are produced through hind leg stridulation and are controlled by complex neural and hormonal mechanisms. Brain neuropeptides and neurotransmitters exert short-term regulation on sound production in *C. biguttulus*, as reviewed previously.[32] Additionally, in *S. gregaria*, neuropeptide F enhances male copulation behavior.[27] However, the roles of neuropeptides and neurotransmitters in visual, olfactory, and tactile mating cues remain poorly understood.

TABLE 1 The regulatory roles of neuropeptides in locust reproduction.

Class	Name	Functions in gonad maturation	Refs
Parsins	OMPs	Increases circulating vitellogenins to stimulate the oocytes' development	23
	IRPs	Upregulates vitellogenin expression in the fat body to promote the ovarian development	24
	NPs	Delays vitellogenesis and suppresses accessory gland maturation probably through the antijuvenile hormone and antidiuretic effects	24–26
Others	NPF	Accelerates oocytes' development promotes the development of male testes and seminal vesicles, and increases the fertilization rate of the progeny eggs	20, 27
	AKH III	The AKH III/AKHR (receptor of AKH III) complex promotes vitellogenesis, probably by upregulating the expression of *Vg* and promoting mobilization of triacylglycerol and trehalose.	28
	ACP	Reduces the fecundity of *Locusta migratoria*, probably by regulating lipid metabolism of the fat body	29

Abbreviations: ACP, adipokinetic hormone/corazonin-related peptide; AKH III, adipokinetic hormone III; IRPs, insulin-related peptides; NPF, neuropeptide F; NPs, neuroparsins; OMP, ovary maturating parsin.

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2.2.3 | Neuropeptides and neurotransmitters control the contraction of reproductive tissues

Fertilization involves the coordinated contractions of reproductive tissues to facilitate sperm transfer via the spermatophore, ovulation of oocytes, and eventual fertilization in the genital tract. Previous reviews summarized the roles of biogenic amines, including serotonin, octopamine, and tyramine, as well as the functions of neuropeptides such as FMRFamide-related peptides, proctolin, crustacean cardioactive peptide, and allatostatin in controlling these contractions to ensure the success of fertilization.[9] Other studies revealed tyramine's role in spermathecal contractions and the opposing effects of octopamine and proctolin on oviduct contractions.[33,34] In addition, neuropeptides and neurotransmitters regulate the female egg-laying behavior by controlling ovipositor opening, oviduct contractions, and ventral protractors of the abdominal segment.[9] All the above neuropeptides and neurotransmitters are necessary for producing a sufficient number of viable locust offspring. However, the involvement of other neurotransmitters such as dopamine, which regulates aggregation behavior in *L. migratoria*,[21] in the contraction of reproductive tissues remains unknown.

Therefore, the neuropeptides and neurotransmitters regulate multiple aspects of reproduction. Pharmacology and RNAi experiments provide versatile and reliable technical platforms for functional studies, whereas CRISPR-associated protein 9 (CRISPR-Cas9) technology enables stable phenotypic validation.[29] Future research should explore additional regulatory pathways involving neuropeptides, neurotransmitters, and their receptors in locust and grasshopper reproduction.

2.3 | Multifunctional integrative genes

Beyond classical hormonal and neural pathways, emerging evidence reveals the involvement of diverse molecular players in locust and grasshopper reproductive regulation.

2.3.1 | Multiple pathways involved in male and female reproduction

Firstly, energy metabolism is tightly linked to insect reproduction.[35,36] The lipid metabolism regulating gene *fatty acid synthase 2*, carbohydrate metabolism gene *FoxO*, and glucose/lipid metabolism gene *glucose transporter 4* (*Glut4*) mediate the ovarian development of *L. migratoria*, probably by influencing the expression of *Vg*.[37–39] Additionally, multifunctional genes such as the circadian clock genes *period* (*per*) and *timeless* (*tim*) can regulate the ovarian development and fecundity of female *S. gregaria*.[40]

Reproductive research has primarily focused on females, with limited studies on males. Many evolutionarily conserved genes exhibit some distinct functions in the male reproduction of locusts and grasshoppers. For example, although circadian genes *per* and *tim* cannot affect the number of sperm, sexual maturation, and copulation behaviors in *S. gregaria*, they may influence male fertility by regulating sperm viability or transfer.[37] Another insect-conserved gene, *fruitless* (*fru*), which is necessary for the sex-specific behaviors in *Drosophila*, controls the generation of a normal number of spermatozoa and male copulation behaviors in *S. gregaria*.[41,42] The c-kit, a cell surface protein that plays crucial roles in mammalian spermatogenesis, also shows strong expression in primary spermatocytes, secondary spermatocytes, and mature sperm in locusts. Additionally, c-kit displays differential expression levels among three species of locusts, *Euchorthippus unicolor* (Ikonn.), *Euchorthippus vittatus* Zheng, and *Omocestus viridulus* (Linnaeus), implying the role of c-kit in reproductive isolation among the three species.[43] Beyond genetics, key spermatogenic processes involve actin/myosin-mediated spermatocyte mitosis.[44] Intriguingly, a specialized tissue, named fat body-like tissue (FLT), surrounding the testis follicles is crucial for the spermatogenesis in *L. migratoria*,[45] although the mechanistic role of FLT remains unknown. Finally, male fertility in *L. migratoria* is age-dependent, with sperm quantity and viability peaking at sexual maturity (~14 days after adult emergence), followed by a decline pattern with aging.[46]

A variety of regulators, beyond neuropeptides and neurotransmitters, are involved in male-female cooperation to ensure reproductive success in grasshoppers and locusts. First, communications via chemical signals regulate mating behavior. For instance, males of *C. biguttulus* and *Chorthippus mollis* use species-specific cuticular hydrocarbons to distinguish conspecific females from heterospecifics/conspecific males.[47] Similarly, in *S. gregaria*, pentanoic acid released from female Comstock–Kellogg glands elicits male precopulatory behavior.[48] Because the male-specific pheromone 2-heptanone induces opposite behavioral responses between males and females in *L. migratoria*, its involvement in copulation behavior is to be determined in the future study.[49] Other chemical molecules, such as pheromones that play crucial roles in male-female communications and are involved in population density-regulated reproduction, are summarized in Section 3.1. Furthermore, bioactive molecules from the MAG play essential roles in intersexual interactions. For instance, the neuropeptides Lom-AG-myotropin I and II (Lom-AG-MT I/II), identified in the MAG, stimulate female oviduct contraction in *L. migratoria* in vitro. This suggests these neuropeptides mediate male-female

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cooperation during copulation.[50] Oviposition-stimulating proteins in the MAG are transferred to females to stimulate oviposition in *L. migratoria* and *M. sanguinipes*.[51,52] Other seminal fluid proteins from the MAG, such as ejaculate serine protease and angiotensin-converting enzyme, are implicated in sperm metabolism and female oviposition.[53] Intriguingly, certain MAG proteins or peptides can be transmitted to progeny eggs and localize in the germ band, suggesting a potential role in early embryogenesis of *L. migratoria* and the grasshopper *Eyprepocnemis plorans*.[54,55] Additionally, sexual reproductive success is also influenced by environmental stressors, which can disrupt the above-described intersexual cooperative processes. Irradiated males produce significantly fewer offspring, probably due to a reduced number of sperm transferred to females. Based on this, sterile insect technique can be applied to control locust populations.[56] Under heat shock, the grasshopper *Spathosternum prasiniferum* exhibits a sex-specific stress response, with heat-shock protein (Hsp) 70 being abundant in ovaries and MAGs and Hsp64 in testes. These protective strategies sustain reproductive system functionality in both sexes, enabling successful female-male reproductive cooperation.[57]

Taken together, although grasshoppers and locusts utilize evolutionarily conserved mechanisms similar to those in other insects, the peculiar features such as FLT and the intergenerational transfer of MAG proteins warrant further investigation.

2.3.2 | Multiple pathways involved in development of progeny eggs

The development of progeny eggs forms the foundation of locust plagues. Embryogenesis and the physiological activities of embryos are mediated through multiple pathways.

Grasshoppers and locusts exhibit a phylogenetically primitive mode of embryogenesis known as short germ development, in which only the head segments form prior to gastrulation. This mode is different from *Drosophila*'s long germ development, where most body segments are generated at the syncytial blastoderm preceding gastrulation.[58] Although most evolutionarily conserved genes participate in embryonic patterning of both *Drosophila* and locusts, many display different expression patterns or functional modes between locust and *Drosophila* embryos (Table 2). Additionally, classical marker genes such as *Vasa* are applied to trace cell origins in *S. gregaria* embryos.[65] The spatiotemporal expression of these conserved genes is well documented, yet their regulatory roles in embryogenesis remain to be fully elucidated.

Recent application of optical coherence tomography in *L. migratoria* enables noninvasive monitoring of embryonic development. It allows access to embryo phenotypes caused by gene modification and facilitates dynamic phenotypic assessment and cardiac analysis.[66,67] This technology facilitates more in-depth studies of environment-regulated embryonic physiology.

TABLE 2 Divergent and conserved functions of embryogenesis genes in locust and *Drosophila*.

Gene name	Similarities to *Drosophila*	Differences from *Drosophila*	Refs
hunchback (*hb*)	Early expression in the position of the germ anlagen and the gnathal/thoracic domain	Maternal *hb* distinguishes embryonic versus extraembryonic cells from embryo development onset.	59
	Later expression in abdominal segments	Zygotic *hb* regulates axial patterning independent of maternal *hb*.	
fushi-tarazu (*ftz*)	-	Lacks pair-rule expression, unlike *Drosophila*	60
even-skipped (*eve*)	-	Lacks pair-rule expression, unlike *Drosophila*	61
paired (*prd*)	Shows a somewhat similar pair-rule expression pattern	-	62
zen	Acts in the establishment of extraembryonic membrane identity	Locust *zen* is maternally transcribed and potentially regulates multiple developmental processes except for extraembryonic membrane specification.	63
caudal	Graded expression pattern at early embryonic developmental stage	The gradient of *caudal* established in locusts is later than in *Drosophila*.	64
wingless (*wg*)	Localizes to cells directly anterior to the parasegment boundary	Locust *wg* shows segmental, not pair-rule, expression as in *Drosophila*.	64
decapentaplegic (*dpp*)	Mediates dorsoventral (D/V) patterning and is essential for sustaining *zen* expression in extraembryonic membranes	Expresses in the necklace cells and is not maternally regulated	64

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For example, the optimal condition for inducing egg diapause, a physiological phenotype in which insect embryo development is arrested to overwinter in the field, is assessed. Combining adult short photoperiod with low egg temperature is the optimal diapause induction condition, whereas a near developmental threshold low temperature effectively terminates diapause.[68] Multiomics studies identified diapause-associated genes, including those involved in hormone biosynthesis, peroxisomes, and energy metabolism.[69–71] RNAi experiments demonstrated that maternal-induced embryonic diapause is mediated by DH-like neuropeptides, as well as insulin pathway regulators such as PTP1B and PTK, and *serpin* genes (Figure 1).[72–75] Respiration is another basic physiological activity essential for the survival of embryos. Unlike nymphs and adults that rely on tracheal systems, embryos depend on haemocyanins Hc1 and Hc2 for oxygen delivery and hypoxia adaptation in *L. migratoria* (Figure 1).[76,77] Other genes are gradually discovered to play a role in embryo physiological activity. For instance, the chitinase 5–1 mediates lamellar procuticle degradation at the end of embryo development.[78] However, the intricate regulatory mechanisms exerted by the above genes are not well understood.

In summary, locust and grasshopper embryos serve as ideal models for studying developmental regulation and environment–embryo interactions in non-*Drosophila* insects. More technical platforms, including development of specific antibodies, microscopic imaging, and physiological monitoring systems, need to be further optimized in future studies.

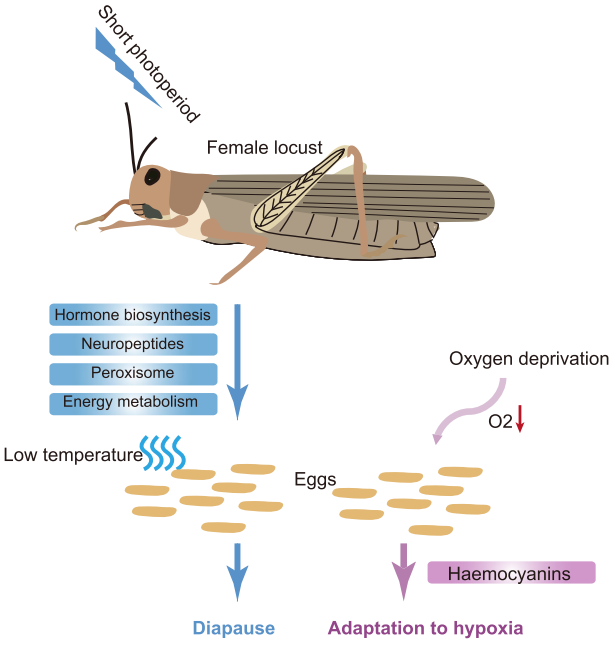

FIGURE 1 Environmentally regulated locust reproduction. Photoperiod in adult females and low temperature in progeny eggs induce diapause through multiple pathways (blue arrows, left). Meanwhile, haemocyanins in the eggs enhance hypoxia resistance by sensing oxygen levels (purple arrows, right).

2.4 | Epigenetic factors regulate the development of reproductive system

microRNAs (miRNAs) are among the most extensively studied epigenetic modulators in regulating reproductive systems across diverse insect species. Previous reviews summarized miRNA-regulated reproduction through hormone signaling and other related pathways.[79,80] Recent studies identified miRNAs that act upstream of the JH signaling pathway. Two miRNAs, miR-276 and miR-182013-5p, inversely regulate the expression of *Jhamt*, which encodes the rate-limiting enzyme in JH biogenesis, although both miRNAs simultaneously target *Jhamt*. miR-276 and miR-182013-5p display low and high expression levels in adult CA, respectively, thereby stimulating the biogenesis of JH in adult locusts.[81] Another six miRNAs, miR-1-3p, miR-9-5p, miR-31a, miR-282, miR-315, and miR-971-3p, inhibit the expression of JH biogenesis genes in the CA. The dynamic expression changes of these six miRNAs in different reproductive developmental stages ensure stage-specific JH titers in female locusts.[82]

Beyond miRNAs, the Piwi-interacting small RNAs (piRNAs) biogenesis factor, Tudor domain-containing protein 5, participates in the ovarian maturation and sperm production of *L. migratoria*.[83] In *E. plorans*, a representative species harboring the supernumerary B chromosome, transcriptional inactivation of both B and X chromosomes occurs in spermatogonia prior to meiosis initiation. The inactivation is accompanied by epigenetic modifications, including histone H2AX phosphorylated at serine 139 (γ-H2AX) and histone H3 trimethylated at lysine 9 (H3K9me3).[84,85] These findings imply linkages between chromatin modifications and spermatogenesis processes. However, further research is needed to elucidate more intricate epigenetic regulatory pathways in locust reproduction, especially in male reproductive functions.

3 | POPULATION DENSITIES REGULATE REPRODUCTION

Owing to the remarkable responsiveness to external stimuli, locusts and grasshoppers serve as premier models for studying integrative signaling pathways from environmental cues to physiological regulation. Reproduction of locusts and grasshoppers can be influenced by temperature, photoperiod, and other environmental factors, as mentioned in the above sections. Moreover, population density-regulated reproductive plasticity of locusts has attracted significant research interest. A recent review addressed the trade-off between reproductive strategies and long-distance migration as adaptive responses to density changes.[5] In this section, we reorganize the literature advances and incorporate

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several previously unmentioned studies to elucidate how population density affects contemporary reproductive fitness and transgenerational phenotypes.

3.1 | Population density regulates adult reproductive strategies

High-density gregarious locusts allocate substantial energy to long-distance migration at the expense of fecundity, whereas low-density solitarious locusts prioritize reproductive investment to ensure population sustainability. The two phases of locusts adopt different strategies throughout various key stages of reproduction, spanning from sexual maturation to egg deposition.

3.1.1 | Sexual maturation and mating behavior

Firstly, the sexual maturation of locusts exhibits distinct characteristics that vary with population densities. Although studies report inconsistent effects on the female maturation speed of *L. migratoria*,[86–90] the acceleration effect of high density on female ovary development is confirmed in both *L. migratoria* and *S. gregaria*.[87,89,90] Gregarious *L. migratoria* females express a higher level of the vesicle transport gene *syntaxin 1A* (*Syx1A*) in the fat body, enhancing the secretion of Vg into the hemolymph and its subsequent uptake by the ovaries. As a result, gregarious females exhibit accelerated oocyte development compared to their solitarious counterparts.[89] Interestingly, except for *Syx1A*, nutritional signaling pathway genes exhibit differential expressions between gregarious and solitarious locusts at previtellogenesis,[89] although the nutrient quality does not differ between the two phases of locusts under laboratory conditions. Considering the essential role of nutrient-promoted fat body remodeling in ovary development,[10] the linkages between population density and nutritional signals in the regulation of oocyte maturation are worthy of further exploration.

Although the sizes of testicular follicles and MAG are greater in solitarious locusts, sexual maturation is delayed in solitarious males compared to gregarious males. This is evidenced by both the earlier sperm accumulation in seminal vesicles and the initiation of mating behavior in gregarious males.[87,91] Male sexual maturation is affected by the combined effects of hormones, neuropeptides, and other regulators. High density induces a high titer of ecdysteroids, which may regulate the production of accessory gland proteins and promote spermatogenesis.[92] Conversely, solitarious males display reduced JH sensitivity or lower JH titers, leading to suppressed secretory activity of MAG.[93] Neuropeptides that exert a positive effect on reproductive development, such as pacifastins, are present at lower levels,[94] whereas those exerting a negative effect, such as NPs, display higher levels in solitarious males.[95] Chemical volatiles released by mature males can promote the maturation of young males of gregarious locusts, both in *L. migratoria* and *S. gregaria*.[96] Additionally, gregarious *S. gregaria* males exhibit greater sperm storage in seminal vesicles, potentially mediated by unidentified male pheromones.[97] Moreover, gregarious males promote synchrony in female sexual maturation via 4-vinylanisole (4-VA), a pleiotropic pheromone that also acts as an aggregation pheromone in *L. migratoria*.[98–100] Male-emitted 4-VA binds to the odorant receptor 35 in females to induce synchrony in ovary development and oviposition.[98] In summary, gregarious locusts apply rapid and synchronized sexual maturation (Figure 2). Interestingly, 4-VA triggers ovarian development through the JH-Vg pathway,[98] which appears to conflict with earlier results that solitarious females display higher JH titers than gregarious females at a specific period in *L. migratoria*.[101] Nevertheless, a comparison of JH titers over an extended stage of *S. gregaria* females revealed consistently higher JH levels in gregarious locusts compared to their solitarious counterparts. Taken together, gregarious males prioritize rapid maturation for swarm synchronization, whereas solitarious males delay reproduction to adapt to sparse mating opportunities.

Mating behavior is another necessary step in reproduction. Solitarious locusts optimize mating efficiency at low densities, with males increasing premount signaling and females showing reduced rejection behaviors in *S. gregaria*.[102] Interestingly, solitarious females can mate with males regardless of ovarian developmental stage. In contrast, the transient locusts, which display gregarious behaviors but with solitarious morphology, employ a "lekking system" to reduce male mating harassment.[103] Furthermore, pheromonal regulation plays crucial roles in different mating behaviors of gregarious and solitarious locusts. Solitarious females release specific sex pheromones, dibutyl phthalate (DBP), to attract males in *L. migratoria*. DBP induces electrophysiological responses in males by specifically binding to the receptor odorant receptor 13 in basiconic sensilla.[104] Gregarious males may use phenylacetonitrile (PAN) to avoid mating competition from other males in *S. gregaria*[105] (Figure 2), although PAN functions as interspecific predator deterrence and intraspecific cannibalism suppression in *L. migratoria*.[106,107] Moreover, carotenoid-binding "yellow protein" (YP)-mediated yellow body color, in conjunction with PAN in gregarious sexually mature males, prevents mistaken sexual harassment from other males of *S. gregaria*.[108] Interestingly, phase-specific attraction in *L. migratoria* may involve headspace volatile compounds,[109] yet mating between gregarious and solitarious locusts still occurs through unknown mechanisms.[110] Therefore, the adult locusts employ context-dependent tactics to regulate sexual

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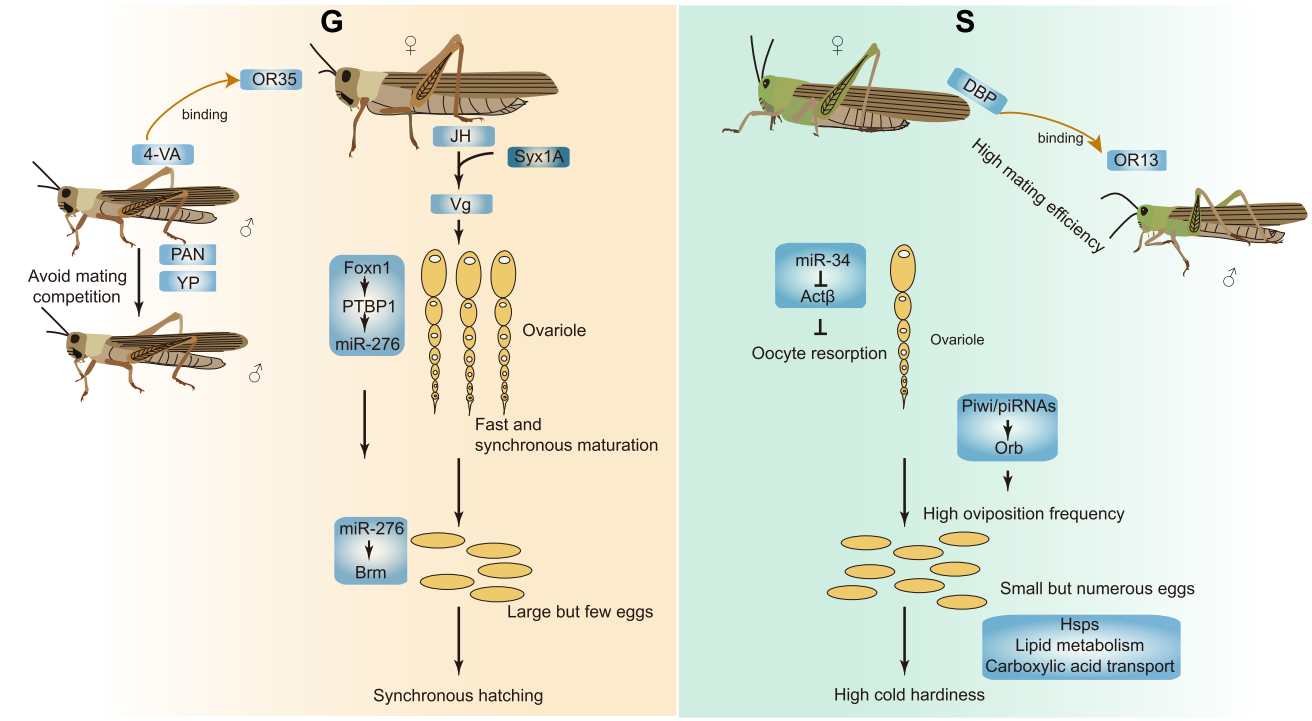

FIGURE 2 Population density-regulated locust reproduction plasticity. Mating behavior: In high population density, gregarious males use PAN and YP to avoid male-male harassment. In low population density, solitarious females release DBP to attract males via the receptor OR13. Oocyte development: In gregarious locusts, 4-VA released from males binds to OR35 in female antennae, triggering synchronized oocyte maturation via the JH-Vg pathway. Simultaneously, higher expression of *Syx1A* enhances Vg secretion and further accelerates oocyte development, resulting in larger eggs. Egg production and transgenerational effects: Solitarious locusts suppress oosorption via the miR-34-Actβ pathway to increase egg numbers, while also enhancing oviposition frequency via Piwi/piRNA-mediated Orb upregulation. In gregarious locusts, high population density activates FOXN1-driven transcription of *Ptbp1* in oocytes, promoting miR-276 biogenesis. Subsequently, miR-276 upregulates the target gene *Brm*. Abundant miR-276 and Brm are transmitted to progeny eggs, ultimately inducing the synchronous hatching of gregarious locust offspring. Solitarious locusts enhance the offspring cold hardiness through Hsps, lipid metabolism, and carboxylic acid transport pathway. 4-VA, 4-vinylanisole; Actβ, activin β; Brm, brahma; DBP, dibutyl phthalate; FOXN1, forkhead box protein N1; JH, juvenile hormone; miR-276, microRNA-276; miR-34, microRNA-34; OR13, odorant receptor 13; OR35, odorant receptor 35; Orb, oo18 RNA-binding protein; PAN, phenylacetonitrile; piRNAs, Piwi-interacting small RNAs; PTBP1, polypyrimidine tract-binding protein 1; Syx1A, syntaxin 1A; Vg, vitellogenin; YP, yellow protein.

maturation and sexual behaviors. The regulatory networks involving more pheromones and genetic factors require further elucidation.

3.1.2 | Fecundity

The solitarious locusts have higher fecundity compared with gregarious locusts in both *L. migratoria* and *S. gregaria*, with more egg pods and greater egg numbers per pod.[89,111–113]

The higher number of egg pods is allocated to the higher oviposition frequency of solitarious females.[111,112] In *L. migratoria*, the oviposition frequency of solitarious locusts is enhanced by Piwi/piRNAs abundant in ovariolar tips. piRNAs upregulate the target gene *oo18 RNA-binding protein* (*Orb*) through pre-mRNA splicing, coordinated with splicing factors.[112] Orb, a key oogenesis regulator in *Drosophila*, shows conserved function in accelerating locust oviposition[112,114] (Figure 2). Interestingly, the mechanism of piRNA-mediated pre-mRNA splicing was also discovered in locust brain,[19] establishing *L. migratoria* as an ideal model for piRNA study.

The number of eggs per pod is determined by two key factors: the total ovariole number and the oocyte resorption (oosorption) ratio. Although the ovariole count does not differ between gregarious and solitarious females in both *L. migratoria* and *S. gregaria*,[113,115] the oosorption rate serves as the pivotal modulator of the number of eggs per pod. Oosorption, a form of follicular regression that prevents specific oocytes from progressing to ovulation due to oocyte death/apoptosis, is regulated by the miR-34 family in *L. migratoria*. Higher expression of miR-34 leads to suppression of the target gene *activin β* (*Actβ*), thereby minimizing resorption and increasing egg number per pod in solitarious females (Figure 2).[113]

In summary, the low fecundity of gregarious locusts supports long-distance migration and reduces offspring

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competition within the group. In contrast, the high fecundity of solitarious locusts results in gradual population accumulation, which ensures population sustainability and ultimately paves the way for pest outbreaks.

3.2 | Density experiences induce transgenerational effects

The density experiences not only can regulate the reproductive phenotypes of adult locusts but also can affect progeny morphology, physiology, and hatching traits.

3.2.1 | Morphological characteristics of offspring

The trade-off between the number of eggs per pod and egg size results in variation in locust egg sizes. Gregarious locusts produce fewer but larger eggs, whereas solitarious locusts yield more but smaller eggs.[89,90] The larger eggs produce larger embryos and final hatchlings in gregarious locusts compared to solitarious ones, due to higher yolk protein content and greater volume.[116] The egg size may be regulated by multiple pathways. Higher expression of *Syx1A* in gregarious females increases the yolk protein content in the ovaries and progeny eggs, resulting in larger-sized eggs (Figure 2).[89] Although the maternal effects dominate, paternal density experience also influences progeny egg size in *L. migratoria*. Additionally, the expression patterns of *Hsps* can be transmitted from male locusts to progeny eggs.[117]

Parental density experiences can regulate hatchling morphology. For *L. migratoria*, high-density parents produce hatchlings with reduced femur/head width ratios (F/C), mirroring adult differences between gregarious and solitarious locusts.[117] For *S. gregaria*, body color of hatchlings is controlled by maternal effects. The hatchlings from gregarious females display a dark or black pattern, whereas the hatchlings from solitarious females are light pale green, a color dimorphism persisting throughout later stages.[118] Although proposed mediators include foam plugs or ovarian factors, the mechanistic basis remains unresolved, as reviewed previously.[119]

3.2.2 | Physiological characteristics of progeny eggs

Cold hardiness, crucial for the eggs to overwinter, displays remarkable maternal effects in locusts. Specifically, solitarious females produce smaller but more cold-resistant eggs than gregarious females, thereby enhancing offspring survival despite their reduced size. Transcriptomic analyses reveal that eggs from solitarious females show upregulation of lipid metabolism-related genes, whereas those from gregarious females exhibit increased expression of *Hsps* and neurotransmitter metabolism genes.[110] Notably, these pathways are also associated with egg diapause, a necessary overwintering strategy in the wild. For instance, energy metabolism pathways are activated, whereas *Hsp* expression is suppressed in diapausing eggs.[70,71] These findings suggest that low temperature and low density may coordinately promote egg diapause, whereas low temperature and high density may exert antagonistic effects. Further studies are needed to unveil the relationships between population density and other environmental cues in regulating the physiological characteristics of progeny eggs.

3.2.3 | Hatching characteristics

Hatching characteristics of progeny eggs are regulated by parental density experiences. Although rain and vibration signals between the eggs provide proximate signals for egg-hatching synchrony of locusts,[3,120] high population density plays a crucial role in parent-regulated fast and synchronous hatching of progeny eggs.[121,122] Egg-hatching synchrony in gregarious locusts represents an adaptive strategy that facilitates subsequent developmental synchrony in nymphs and adults. The miRNA pathway transduces parental density signals to control egg-hatching synchrony. The highly expressed transcription factor forkhead box protein N1 activates the transcription of *polypyrimidine tract-binding protein 1* (*Ptbp1*) in the oocytes of gregarious females. The PTBP1 is an RNA-binding protein that can recognize the "CU motif" in the precursor of miR-276 (pre-miR-276). By associating with the miRNA export factor exportin 5 (XPO5), PTBP1 promotes the nuclear export of pre-miR-276, resulting in high efficiency of miR-276 biogenesis.[4] The abundant miR-276 is transmitted to progeny eggs and upregulates target *brahma* (*Brm*), which encodes an essential transcription coactivator in embryo development, promoting egg-hatching synchrony.[4,121] Intriguingly, miR-276 upregulates *Brm* by unwinding the RNA stem-loop structure, a noncanonical manner by which miRNA modulates the target gene expression (Figure 2).[121]

Collectively, elucidation of the signaling pathway linking adult density experiences to progeny eggs deepens the insights into locust swarm formation. Up to now, the prevalence of maternal density experience-regulated offspring phenotypes is well-known, with stronger effects on egg size and hatchling morphology than paternal contributions.[117] Similarly, modification of miRNAs in females alters hatching synchrony in gregarious locust eggs.[4,121] However, non-negligible paternal effects exist in locusts, underscoring the evolutionary significance of this effect. Paternal effects in locusts remain poorly understood, with critical gaps in

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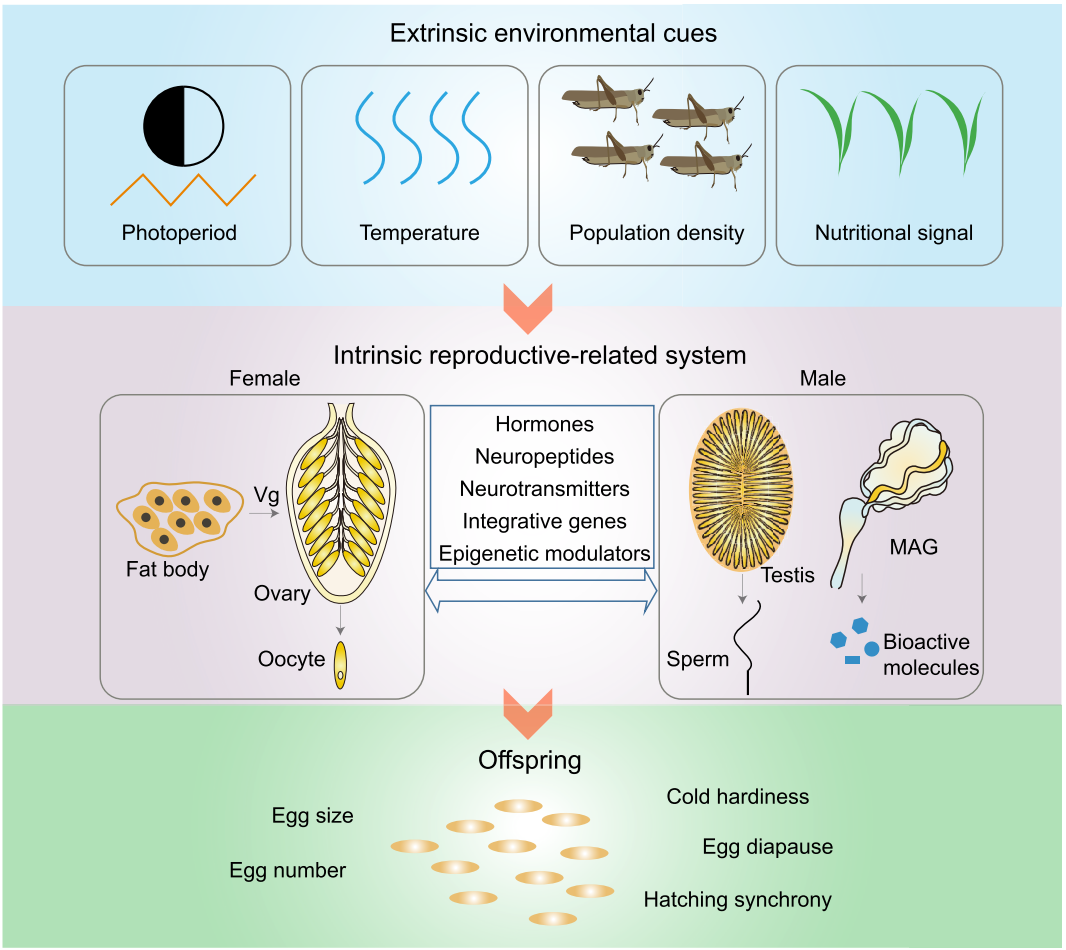

FIGURE 3 The model of the extrinsic environmental cues-intrinsic gonadal system-transgenerational reproductive phenotypes regulatory pathway. Environmental signals such as photoperiod, temperature, population density, and nutritional signals initiate responses in intrinsic reproductive-related tissues of adult locusts and grasshoppers. Signal transduction involves a suite of regulators, including hormones, neuropeptides, neurotransmitters, integrative genes, and epigenetic modulators. In the female, environmental signals regulate ovarian development either via the fat body (through vitellogenesis) or via fat body-independent mechanisms. In the male, environmental signals modulate the development of testes and MAG, thereby affecting their function. Ultimately, environmental signals are transgenerationally transmitted to offspring via oocytes, sperm, and MAG-derived bioactive molecules, influencing egg size, egg number, cold hardiness, egg diapause, and egg-hatching synchrony of offspring. MAG, male accessory gland; Vg, vitellogenin.

both transmission mechanisms and downstream impacts. On one hand, the role of paternal molecules in shaping offspring traits is well documented in other taxa, such as sperm-borne small RNAs mediating metabolic programming in mammals, or male nutrition altering offspring metabolism in the neriid fly *Telostylinus angusticollis*, and male infections modulating offspring immunity in the red flour beetle *Tribolium castaneum* via seminal fluid.[123–125] In locusts and grasshoppers, knowledge of transmission pathways of paternal epigenetic molecules is limited, despite evidence that MAG proteins are transferred to progeny embryos.[54,55] On the other hand, paternal *Hsps* may theoretically act as epigenetic regulators in locusts, based on the established role of Hsp90 in chromatin remodeling and heritable transcriptional changes.[126] However, direct evidence in locusts is lacking. Additionally, although paternal and maternal effects jointly regulate progeny egg size in locusts,[117] it remains uncertain whether these effects might counteract each other under certain conditions. Taken together, a comprehensive analysis of the molecules in locust sperm and seminal plasma, as well as the transgenerational effects induced by these molecules, remains to be conducted.

4 | CONCLUSION AND PERSPECTIVES

Integrated actions of classical regulatory factors and noncanonical regulatory pathways coordinately modulate the reproduction of locusts and grasshoppers. Over the past decades, the findings have established these insects as ideal non-*Drosophila* models for studying

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reproductive regulation. Especially, locusts exhibit typical advantages for exploring the responsive signaling pathways from external environmental cues, such as photoperiod, temperature, nutritional signals, and population density, to the internal reproductive-related tissues and progeny eggs (Figure 3). The genome mapping of *L. migratoria* and *S. gregaria* promotes the investigation of the molecular regulation pathways of reproduction.[127,128] Recent chromosome-level genome assembly of *L. migratoria* will further propel the elucidation of reproductive mechanisms.[129]

These advances not only deepen our understanding of reproductive regulation but also provide theoretical foundations for novel pest management strategies. For example, noncoding small RNAs, which possess multiple advantages, such as the ability to transfer from female oocytes to progeny eggs and superior synthetic feasibility, represent promising targets for disrupting pest reproduction. Additionally, species-specific pheromones involved in reproductive regulation offer powerful tools for targeted pest control.

Despite significant progress in identifying reproduction modulators in locusts and grasshoppers, more efforts are required to devote to the regulatory mechanisms and pest control technologies. First, although small RNAs have been the primary focus of epigenetic studies in locust reproduction, the functions of other epigenetic modulators remain unclear. Recent studies revealed the patterns of genome methylation and histone modification in the reproductive system, as well as the functions of long noncoding RNAs, RNA modification, and chromatin accessibility in phenotypic plasticity of locusts,[130–136] thereby underscoring the potential importance of various epigenetic modulators in reproductive regulation. The above-mentioned regulatory mechanisms present promising avenues for future studies on reproduction regulation. Furthermore, beyond *L. migratoria* and *S. gregaria*, more attention should be directed to other agriculturally significant grasshopper species. The development of multiomics could accelerate discoveries in this field. More importantly, technical challenges remain non-negligible for the translation of research findings into IPM strategies for locusts. For instance, RNAi-based manipulation of gene expression in the female ovary is not feasible in locusts, probably due to the poor delivery of double-stranded RNA (dsRNA) into the ovary.[137] Although CRISPR-Cas9-based gene knockout has been well established in laboratory locust studies,[99,138] gene overexpression techniques have only been reported in a single study to date.[139] Furthermore, the field application of CRISPR-Cas9 is impeded by delivery inefficiencies and high costs. Additionally, practical challenges related to delivery also exist for small RNA- and pheromone-based pest control. Although transgenic plant-mediated miRNA delivery offers an efficient alternative to counteract the degradation of small RNAs in the air or plant tissues,[140] this approach increases costs and faces strict risk assessments. For pheromones, safe chemical analogs and the development of sustained-release carriers are critical for field deployment.[100,141] Therefore, future breakthroughs should focus on overcoming delivery challenges and reducing costs to advance the field application of RNAi, miRNA, and pheromone-based technologies for controlling locust and grasshopper reproduction.

AUTHOR CONTRIBUTIONS

Jing He: Conceptualization; investigation; funding acquisition; writing—original draft; writing—review and editing. **Jiliang Wang**: Investigation; writing—original draft. **Xinran Wang**: Writing—review and editing; visualization.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during this study.

ORCID

Jing He https://orcid.org/0000-0003-0790-2659

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