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Phenotypic Plasticity in Locusts: Trade-Off Between Migration and Reproduction

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Abstract

Locusts exhibit phenotypic plasticity in response to population density changes, with distinct phenotypes in the solitary and gregarious phases. In the past decade, many studies have revealed the molecular mechanisms underlying phase changes, which include the change of body coloration, pheromones, behavior, flight, fecundity, immunity, and aging. Our understanding of the molecular mechanisms related to these phenotypic differences has expanded in breadth and depth with the decoding of the locust genome, involving transcriptional, post-transcriptional, translational, and epigenetic regulation. Large-scale regulation networks composed of genes and noncoding RNAs reflect the systematic modifications of the locust phase transition in response to environmental changes. Gene manipulation techniques have verified the functions of specific genes and related pathways in phase changes. This review highlights the latest advances in studies of locust phase changes and suggests that the divergence of energy and metabolism allocation in gregarious and solitary locusts is an adaptive strategy for long-distance migration and local reproduction, respectively. Finally, we propose future research directions and discuss emerging questions in the area of phenotypic plasticity of locusts.

1. INTRODUCTION

Locusts are globally significant pests that cause substantial economic losses, social impacts, and environmental consequences. Globally, there are around 25 species of grasshoppers that are considered locusts, which exhibit phenotypic plasticity whereby solitary individuals transition to gregarious individuals that form high-density bands or swarms and engage in long-distance migration (89, 107). However, most efforts over the past two decades have focused on basic and applied studies in just two species: the migratory locust (*Locusta migratoria*) and the desert locust (*Schistocerca gregaria*) (15).

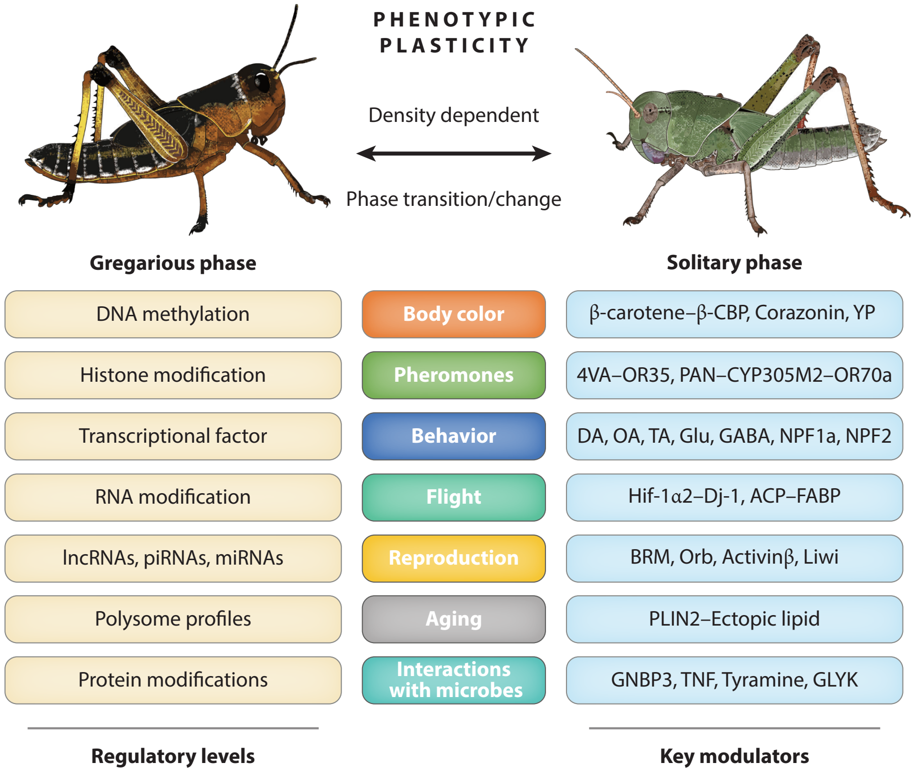
Phenotypic plasticity, also known as polyphenism, refers to the capacity of a single genotype to generate multiple phenotypes in response to varying environmental conditions (60, 111). Locusts exhibit density-dependent polyphenism or phase changes, which are characterized by the reversible transition between gregarious and solitary phases in response to population density change (60, 111). In fact, the phase transition of locusts, which was discovered by Boris P. Uvarov one century ago (122), is a typical phenomenon of phenotypic plasticity (132). Phase transition has been regarded as one of the most important strategies for the successful adaptation of locusts and the underlying cause of outbreaks of locust plagues. Low-density solitary locusts invest more in reproduction to counteract the risk of small-population extinction. By contrast, gregarious locusts, which form swarms, must contend with the challenges of resource scarcity and disease risk and develop long-term migration to access more food and spawning resources. Therefore, locusts in different phases exhibit a remarkable divergence of multiple phenotypes (89, 115, 132) and employ various adaptive strategies in response to the changing environment, all in the shared goal of survival. The different adaptive strategies between solitary and gregarious locusts are associated with multiple phenotypes, which are regulated at different molecular levels.

Over the past decade, there has been a significant increase in the number of research articles focused on locust and grasshopper biology and control technologies, highlighting the importance of these species in biology (with more than 5,500 articles published, according to data from Web of Science). During this period, there were about 90 research articles on locust polyphenism published. We chose to focus on the current research progress in phase changes of locusts, rather than on broad biology and management technologies that have been reviewed by other scientists (15). Although a specialized review article on molecular mechanisms of locust phase changes was published 10 years ago (132), significant progress has been made in understanding the molecular mechanisms underlying the locust phase transition, including genetic and epigenetic regulation, over the past decade (**Figure 1**). In this review, we highlight the research advances in multiple aspects of locust polyphenism or phase changes, which address the strategic divergence between long-distance migration and local reproduction in response to changes in population densities.

2. FACTORS TRIGGERING LOCUST PHASE TRANSITION

Density-dependent phenotypic plasticity is expressed in locust species belonging to at least six different subfamilies within Acrididae and encompasses numerous density-dependent reaction norms (106). Although locust polyphenism has evolved multiple times within Acrididae, similar phase traits are shared among closely related species from a phylogenetic perspective. The similarities among locust species can be attributed to shared ancestry, while the differences can be attributed to the different rates at which certain components of locust polyphenism have evolved (106–108).

The most fundamental factor triggering locust phase transition is population density. At a large scale, temperature, precipitation, and resource distribution can all influence locust synchronized activity and development and, consequently, induce an increase in local population density in the



Regulatory levels		Key modulators
DNA methylation	Body color	β-carotene–β-CBP, Corazonin, YP
Histone modification	Pheromones	4VA–OR35, PAN–CYP305M2–OR70a
Transcriptional factor	Behavior	DA, OA, TA, Glu, GABA, NPF1a, NPF2
RNA modification	Flight	Hif-1α2–Dj-1, ACP–FABP
lncRNAs, piRNAs, miRNAs	Reproduction	BRM, Orb, Activinβ, Liwi
Polysome profiles	Aging	PLIN2–Ectopic lipid
Protein modifications	Interactions with microbes	GNBP3, TNF, Tyramine, GLYK

Figure 1

Overview of locust phenotypic plasticity and its regulatory network. Locust phenotypic plasticity involves a series of characteristics closely related to survival and reproduction. Multiple coding genes and noncoding RNAs orchestrate a complex network regulating phase changes in locusts. Abbreviations: β-CBP, β-carotene binding protein; 4VA, 4-vinylanisole; ACP, adipokinetic hormone/corazonin-related peptide; BRM, brahma; DA, dopamine; Dj-1, Parkinson disease protein 7; FABP, fatty-acid-binding protein; GABA, γ-aminobutyric acid; Glu, glutamate; GLYK, glycerate kinase; GNBP3, a pattern recognition protein; Hif, hypoxia inducible factor; Liwi, Piwi protein of locusts; lncRNA, long noncoding RNA; miRNA, microRNA; NPF, neuropeptide F; OA, octopamine; OR, odorant receptor; Orb, oo18 RNA-binding protein; PAN, phenylacetonitrile; piRNA, Piwi-interacting RNA; PLIN2, perilipin 2; TA, tyramine; TNF, cytokine tumor necrosis factor; YP, yellow protein.

field (20, 124). In the laboratory, crowding (solitary locusts are forced to live with other individuals in a cage) and isolation (gregarious locusts are kept separated) are effective treatments for altering population density and triggering the phase transition of locust species at morphological (8, 144), physiological (42, 71), and behavioral levels (40, 97). While changes in morphological and physiological traits require a few days to several stadia to take place (8, 144), behavioral changes can occur in just a few hours or a few days depending on the locust species (40, 97). In the migratory locust (*L. migratoria*), behavioral changes in nymphs from the gregarious phase to the solitary phase can rapidly occur; in contrast, the change from solitary to gregarious behavior is slow (40). The desert locust, in contrast to the migratory locust, exhibits faster change from the solitary to the gregarious phase but much slower change from the gregarious to the solitary phase (97). However, the Australian plague locust (*Chortoicetes terminifera*) shows a similar time course in both processes (33). In addition, visual, olfactory, and tactile stimuli from conspecifics can also effectively induce the behavioral phase changes of locusts alone or combined with each other (16, 96, 105).

3. BODY COLORATION

DEGs: differentially expressed genes

Body color polyphenism, characterized by the transition between the green coloration of solitary locusts and the black-brown coloration of gregarious locusts, is one of the most conspicuous phase-related traits, corresponding to changes in population density and behavioral changes (88, 89, 114, 123, 132). The green coloration of solitary locusts serves as a protective camouflage in plants when they are at low density. The black-brown color pattern of gregarious locusts serves as a warning coloration, which is necessary due to the inevitable exposure of large-scale swarms to predators (19, 112). Previously, green and black body colorations were thought to be induced by juvenile hormone (JH) and the neuropeptide [His^7]-corazonin (Crz), respectively (113, 116). Recent research revealed that the body coloration change between solitary and gregarious locusts is regulated by a complex process involving the interaction of pigments and pigment-binding proteins.

Comparisons of the transcription profiles of the green integument of the solitary locust and the black integument of the gregarious locust have identified several differentially expressed genes (DEGs) associated with this color polymorphism. A key DEG encoding a β-carotene-binding protein (βCBP) is highly expressed in gregarious locusts and binds to β-carotene, resulting in the formation of red coloration. The black-colored backs of gregarious locusts are formed by the presence of the red-colored β-carotene (pigment)–βCBP (protein) complex on the green-colored background of solitary locusts, rather than by deposition of melanin (144). This color scheme perfectly fits the principle of three primary colors. Based on this study, Kang et al. (59) further examined the tissue-specific expression patterns underlying the black-brown patterns observed in gregarious locusts. The black and brown coloration of locusts is attributed to varying amounts of β-carotene and βCBP complexes in the integuments, and higher amounts of β-carotene and βCBP complexes appear in the sterna. The changes in amounts of β-carotene and βCBP complexes are controlled by the transcription factor (TF) ATF2, whose phosphorylation levels vary in the pronotum and prosternum and rapidly respond to changes in population density. Phosphorylation of ATF2 mediated by PKCα facilitates the translocation of ATF2 into the nucleus and the transcription activation of βCBP. The spatial variation in ATF2 phosphorylation enables locusts to adapt to changing environment for aposematism (59). In addition, the uniform coloration of gregarious locusts likely facilitates the conspecific identification and migration.

Yellow body coloration is prominent in gregarious nymphs and male adults of desert locusts (*S. gregaria*). Yellow protein of the takeout family, also known as yellow protein (YP), is responsible for yellowing in *S. gregaria* nymphs, and its expression is influenced by temperature and JH and Crz levels (110). Gregarious male adult yellowing acts as an intrasexual warning signal to prevent mistaken sexual harassment from other males during scramble mating in a swarm (17). Socially mediated expression of YP repurposes a nymph signal that deters predators into an adult signal that deters undesirable mates (17).

4. PHASE-RELATED CHEMICAL PERCEPTION

4.1. Key Pheromones

The identification of the aggregation pheromone in locusts has been a topic of significant interest to scientists for more than 50 years. Many compounds have been suggested to be aggregation pheromones of desert and migratory locusts; the chemical phenylacetonitrile (PAN) is the most frequently mentioned compound in the desert locust (82, 84, 121). However, none of these compounds meet all criteria of locust aggregation pheromones.

The chemical compositions and emission dynamics of volatiles from the body and feces in the migratory locust (*L. migratoria*) and their relationships with developmental stages, sexes, and phase changes have been thoroughly explored (139). Among 35 compounds identified, PAN and 4-vinylanisole (4VA) were specifically emitted in gregarious individuals but cannot be detected in solitary locusts (43, 138, 139). In gregarious locusts, the biosynthesis of PAN from phenylalanine is catalyzed by CYP305M2, which is encoded by a (*Z*)-PAOx-specific cytochrome P450 (CYP) gene. The consistent higher expression of *CYP305M2* in gregarious locusts compared to solitary locusts in all stages is responsible for the specific emissions of PAN in gregarious locusts. However, in all behavior assays, PAN does not display any attractiveness to gregarious or solitary locusts, despite being the most abundant volatile chemical in gregarious locusts (138).

Clustered regularly interspaced short palindromic repeats associated protein 9 (CRISPR-Cas9): a well-established gene editing technology

Further investigations demonstrated that PAN functions as an olfactory aposematic signal and cyanide precursor and is responsible for defending against predators (138). Recent research has shown that the absence of PAN in the mutant line of *CYP305M2* leads to increased cannibalism of locusts, while the elevation of PAN in locusts induced strong avoidant behaviors and inhibits cannibalism among individuals (6). Therefore, PAN plays a crucial role in locust aggregation by deterring predators and intraspecific competition, rather than as an aggregation pheromone.

4VA is another chemical specifically emitted in the gregarious phase of the migratory locust (*L. migratoria*) (43, 139). Recently, 4VA has been identified as an aggregation pheromone of the migratory locust through a series of assays at the behavioral, chemical, neural, and field levels (43). 4VA can attract locusts regardless of sex, age, and phase state. Simultaneously, OR35, a specific odorant receptor of 4VA, has been identified, and mutants of *Or35* edited by clustered regularly interspaced short palindromic repeats associated protein 9 (CRISPR-Cas9) lose attraction to 4VA, as well as their aggregative ability. The gregarious-specific emission pattern, with no sex bias and high sensitivity to population density changes, perfectly aligns with the behavioral traits of gregarious locusts and transition between the solitary and gregarious phases. A detailed functional exploration of 4VA in the locust phase change has been made, and the results demonstrated that 4VA exposure contributes largely to the behavioral transition from the solitary to the gregarious phase by enhancing the propensity toward proximity and body contact among conspecific individuals (142). Furthermore, mature gregarious males emit high levels of 4VA, and abundant 4VA release induces sexual maturation synchrony of female locusts (10). Synchronized sexual maturation of female adults facilitates copulation, egg laying, and hatching synchrony and guarantees the high population density of the offspring. Simultaneously, parental phase-related characteristics can be transmitted to the offspring through maternal and paternal effects (8, 45). Thus, gregarious-specific 4VA in the adult stage ensures that the gregarious status from the parents continues into the next generation.

The population dynamics of locusts vary greatly, ranging from solitary individuals to high-density swarms, leading to the divergence of the solitary and gregarious phases. Recent research in the migratory locust found that solitary locusts, but not gregarious ones, heavily rely on dibutyl phthalate (DBP) as a sex pheromone for sexual communication and reproduction (14). DBP is abundantly released by female solitary locusts and elicits greater attraction to male solitary locusts than to male gregarious locusts. Notably, the attractiveness of DBP to male locusts becomes more evident at lower population densities, as demonstrated by studies controlling cage size (14). This discovery indicates the potential utilization of sex pheromones for sexual communication in extremely low-density conditions and provides important insights into alternative approaches for population monitoring of locusts.

4.2. Olfactory Proteins

Inside the sensilla on insect antennae, odorant-binding proteins (OBPs) and chemosensory proteins (CSPs) are responsible for capturing and transporting odorants to activate different types of receptors (86, 87). Odorant receptors (ORs), ionotropic receptors (IRs), and sensory neuron membrane proteins (SNMPs), transmembrane proteins expressed in olfactory receptor neurons housed under the sensilla, allow the transduction of chemical signals into electrical signals and transmission of information to the antennal lobe and mushroom body in brain (63, 109).

ORs: odorant receptors

Numerous genes act as transporters and receptors of olfactory information in the locust phase change. The highly expressed chemosensory proteins (*CSPs*) in the antennae of gregarious locusts and the highly expressed takeout gene (*TO1*) in the antennae of solitary locusts display opposite expression trends during the crowding and isolation processes. The results of RNA interference (RNAi) knockdown experiments demonstrate that *CSPs* and *TO1* regulate the switch between attraction and repulsion during the behavioral phase change of the migratory locust (40). These genes have been further verified to be influenced by JH during the locust phase change (39). The application of the JH analog methoprene can significantly shift the olfactory responses of gregarious locusts from attraction to repulsion in response to the volatiles released by gregarious locusts. Expressions of *TO1* and *CSP3* exhibit the reverse pattern after methoprene injection and knockdown of key genes (*Met* or *Kr-h1*) in JH pathways, respectively (39).

OBPs are thought to play an important role in insects for perceiving odorant molecules. In the desert locust (*S. gregaria*) genome, 14 OBPs have been identified according to the antennal transcriptome (58), and 17 OBPs have been identified in the *L. migratoria* genome (38). In the migratory locust, six OBPs showed higher expression levels in the antenna tissue of gregarious nymphs, and LmigOBP2 and LmigOBP4 expression are positively correlated with crowding and isolation treatments, respectively. RNAi experiments confirm that LmigOBP4 alone regulates the gregarious behavior of locusts (38).

Olfactory sensation is fine-tuned by olfactory receptor genes. Based on the genome and transcriptome of the migratory locusts (131), 142 ORs (including one Orco) and 32 IRs have been identified. Most ORs and IRs display olfactory-specific expression, while several members exhibit broad or internal expression in other tissues (137). The detection of odorants in the migratory locust exhibits low redundancy, in contrast to the broadly tuned ORs found in other insects (7). Knockout or knockdown of *Orco* impairs the perception of most odors and leads to the loss of gregarious behaviors in locusts (67, 137). *Or35* knockdown or knockout can significantly change the responses of locusts to 4VA and results in the behavioral transition from the gregarious to the solitary phase (43, 142). Knockout of *Or70a* leads to the loss of perception for PAN and enhances the conspecific cannibalism of gregarious locusts (6). *Or5* knockout impairs the detection by locusts of and aversive responses of locusts to geranyl acetone (7).

In desert locusts, 119 ORs and two coreceptors for the IRs, IR8a and IR25a, have also been identified (34, 91). Most of these belong to the basal group located in olfactory sensory neurons (OSNs) under the basiconic or trichoid sensilla (91), while IR8a and IR25a specifically are located in the coeloconic sensilla (34). In addition, several ORs coexpress with SNMP1, which may possess a dual function in olfactory signal detection and in sensillum lymph maintenance (5, 90, 91). However, the functional identification of ORs and SNMPs in desert locusts needs to be further explored.

5. NEURAL REGULATION OF PHASE-RELATED BEHAVIORS

5.1. Dopamine Pathway

Dopamine is a well-known and conserved neurotransmitter and plays crucial roles in multiple biological processes in both vertebrates and invertebrates (127). Recently, a series of studies have explored the regulation of the dopamine pathway in phase changes of the migratory locust, with special focus on key enzymes, receptors, and their regulators. In the dopamine pathway, *henna* and *pale* encode two crucial enzymes that catalyze the process of turning phenylalanine into dopamine (61). A previous study revealed that the production of dopamine and the expression of key genes (such as *henna*, *pale*, and *vat1*) are upregulated in gregarious locusts. Pharmacological intervention and RNAi of these key genes can lead to behavioral changes from the gregarious to the solitary phase (61). Subsequently, miR-133 negatively regulates *henna* and *pale* expression by binding their coding region and 3′ untranslated region, respectively. miR-133 agomir delivery can effectively suppress the expression of *henna* and *pale*, which in turn leads to a decrease in dopamine production and, ultimately, results in the behavioral shift from the gregarious phase to the solitary phase (146).

A nuclear-enriched long noncoding RNA (lncRNA), *PAHAL*, can also impact dopamine biosynthesis by regulating phenylalanine hydroxylase (*PAH*, also abbreviated as *henna*) at the transcriptional level in the migratory locust (150). *PAHAL* positively regulates *PAH* expression resulting in increased dopamine production in the brain, and induce locust behavioral aggregation. Mechanistically, *PAHAL* enhances *PAH* transcription by recruiting serine/arginine-rich splicing factor 2 (SRSF2), a transcription/splicing factor, to the *PAH* proximal promoter (128). This lncRNA is inserted by a Gypsy retrotransposon harboring a RNA nuclear localization signal motif, which facilitates the stable accumulation of *PAHAL* in the nucleus. The Gypsy element further offers high-affinity SRSF2 binding sites for *PAHAL*, leading to the recruitment of SRSF2, and subsequently *PAHAL*-mediated transcriptional activation of *PAH* in gregarious locusts (151).

Long noncoding RNA (lncRNA): an RNA >200 nucleotides possessing minimal or nonexistent protein-coding ability that plays an important role in transcriptional regulation and epigenetic gene regulation

microRNAs (miRNAs): endogenous, ∼22-nucleotide RNAs that play crucial regulatory roles in animals and plants by paring to mRNAs of protein-coding genes to direct their post-transcriptional regression

Dopamine receptors mediate the functions of dopamine in diverse biological process (81). Two dopamine receptors, Dop1 and Dop2, have been identified in the migratory locust, and these receptors play different roles in the behavioral phase change between gregarious and solitary locusts. Dop1 promotes gregariousness by increasing locomotion and attraction responses, while Dop2 induces solitariness by reducing locomotion and triggering repellent responses (42). Based on these results, the differentially expressed small RNAs downstream of Dop1 were further screened, and it was found that miR-9a expression is negatively regulated by Dop1. Downregulation of miR-9a in solitary locusts increases their attraction to gregarious volatiles, whereas miR-9a overexpression in gregarious locusts reduces olfactory attraction. Moreover, miR-9a directly targets adenylyl cyclase 2 (AC2), causing its downregulation at the messenger RNA (mRNA) and protein levels, and in turn inhibits locust olfactory attraction. Mechanistically, active Dop1 inhibits miR-9a expression by inducing the dissociation of the La protein from premiR-9a, resulting in miR-9a maturation inhibition (41). These results reveal a precise regulation loop involving coding genes and microRNAs (miRNAs) in which a Dop1–miR-9a–AC2 circuit enhances locust olfactory attraction underlying aggregation (**Figure 2**). Additionally, these findings also suggest that miRNAs act as key messengers in G protein–coupled receptor signaling.

In addition to the crucial genes involved in dopamine biosynthesis and signaling, direct modifications of dopamine as a neurotransmitter have also been shown to play important roles in the phase change of the migratory locust. Dopamine in the brain is identified to be actively sulfate conjugated, and the sulfate conjugation enhances the free dopamine–mediated behavioral aggregation. The role of sulfate conjugation for dopamine is also seen in *Caenorhabditis elegans* and mice, suggesting the existence of a conserved mechanism in which sulfation-mediated modification effectively regulates animal social-like behavioral plasticity (9).

5.2. Neuropeptides

The roles of neuropeptides in locust phase changes have long attracted the attention of scientists. However, direct functional verifications in locust phase changes have only been explored in the past 10 years. Several neuropeptide precursors, such as myosuppressin peptides, calcitonins, neuroparsins, vasopressins, and neoneuroparsins, have been identified on the basis of the Expressed

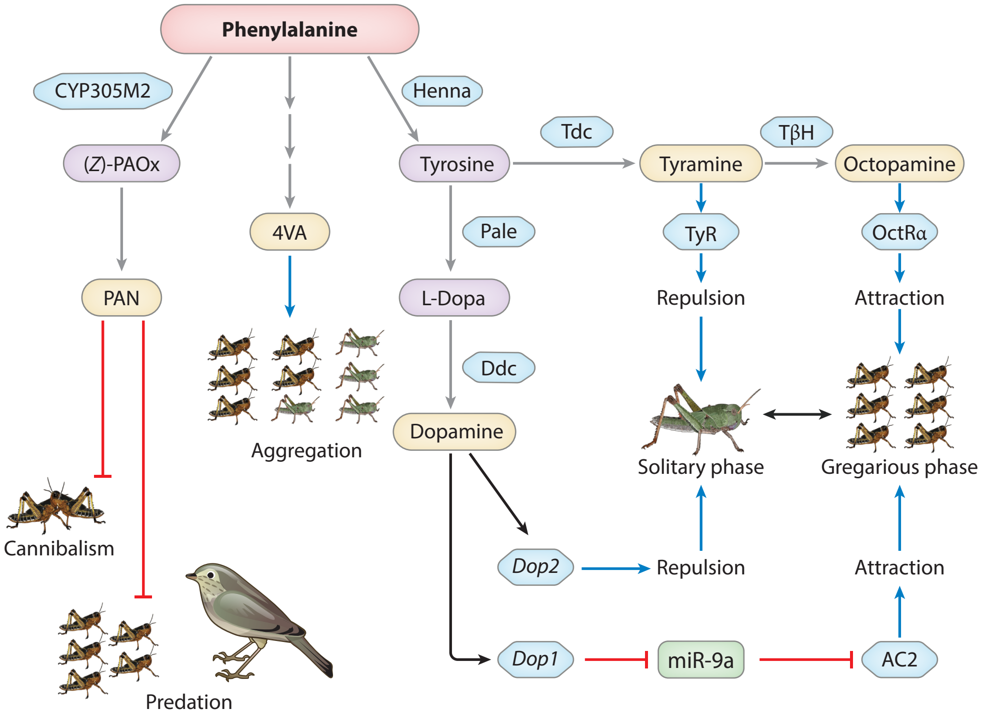


Figure 2

Phenylalanine metabolic pathways play crucial roles in locust phenotypic plasticity. Multiple neurotransmitters and pheromones from phenylalanine work together to form a complex regulatory network that controls the phenotypic plasticity of locusts. Abbreviations: 4VA, 4-vinylanisole; AC2, adenylyl cyclase 2; Ddc, decarboxylase; Dop1/2, dopamine receptor 1/2; Henna (PAH), phenylalanine hydroxylase; OctRα, octopamine receptor α; Pale, tyrosine hydroxylase; PAN, phenylacetonitrile; TβH, tyramine β-hydroxylase; Tdc, tyrosine decarboxylase; TyR, tyramine receptor; (*Z*)-PAOx, (*Z*)-phenylacetaldoxime.

Sequence Tag (EST) database (13) and the contig sequences of *L. migratoria* genome (126). Due to the missing 5′ or 3′ encoding sequences in the prediction, 23 reported neuropeptide precursor genes have been revised and almost all of the neuropeptide precursors and corresponding products identified in the migratory locust (52). Transcriptomic analysis and quantitative polymerase chain reaction data confirmed that most neuropeptide precursors were strongly expressed in the central nervous system. There are 15 neuropeptide genes that display different expression levels between solitary and gregarious locusts (52), suggesting that they have functions in the phase transition of locusts.

Piwi-interacting RNAs (piRNAs): ∼23–30-nt-long RNAs that typically originate from transposable elements in the genome and play important roles in regulating gene silencing through base-pairing recognition

The transcripts encoding two related neuropeptides, NPF1a and NPF2, show reduced levels during crowding, and the numbers of NPF1a and NPF2 receptors significantly increase during locust isolation. Nitric oxide synthase (NOS), a key downstream mediator for both NPFs, regulates phase-related locomotor activity by controlling NO synthesis in the locust brain (55). Furthermore, a conserved TF, CREB-B, has been verified as a key mediator involved in the signaling pathway from NPF2 to NOS, triggering the locomotor activity shift between solitary and gregarious locusts (53). NPF has been reported to play a role in controlling feeding in desert locusts (21, 125). Piwi and Piwi-interacting RNAs (piRNAs) were recently found to regulate NPF-mediated food intake in gregarious migratory locusts. Knockdown of Piwi1 induces decreased expressions of NPF1 in a piRNA-dependent manner and results in the suppression of anabolic processes, as well as the reduction of food consumption and body weight. Mechanistically, intronic piRNAs might enhance RNA splicing of NPF1 by preventing hairpin formation at the branch point sites (130). Additionally, a conserved neuropeptide, [His^7]-corazonin, can regulate both the body coloration and morphometrics in the Central American locust *Schistocerca piceifrons* (27).

5.3. Other Neurotransmitters

Octopamine–tyramine and glutamate–GABA are well known neurotransmitters with close interrelationships in both biosynthesis and function. In the migratory locust, these two paired neurotransmitters exhibit antagonistic functions in the behavioral phase transition (71, 143). Solitary locusts exhibit a preference for gregarious volatiles during crowding, whereas gregarious locusts avoided their volatiles during isolation. Octopamine–octopamine receptor α and tyramine–tyramine receptor mediate attraction and repulsion responses during the phase change, respectively (71). Cellular retinaldehyde-binding protein and translocator protein have been further verified to act as effector proteins downstream of octopamine and tyramine signaling, modulating olfactory responses (72, 73).

Based on a genome-wide screen of differentially expressed miRNAs between two phases of locusts, miR-8–5p was identified and verified to control the GABA–glutamate functional balance by directly targeting glutamate decarboxylase (Gad). The levels of glutamate are higher in gregarious locusts, while solitary locusts enhance GABA levels by increasing the expression of Gad. After feeding with a transgenic rice line expressing the miR-8–5p inhibitor by short tandem target mimic (STTM), Gad transcript levels in the brains of gregarious locusts upregulate greatly, and aggregation behavior is lost (143). Using transgenic plants that express miRNA inhibitors for key genes provides a future potential control approach through behavioral regulation in insect pests.

In desert locusts, several neurotransmitters are also involved in phase characteristics. Serotonin in the thoracic ganglia is considered to be a neurochemical mediating the behavioral phase transition (98, 99). However, there are also alternative results from a different laboratory (117). On the other hand, systematic application of dopamine and antagonists of all dopamine receptor subtypes significantly alter the fast extensor motor neuron responses and induce the behavioral phase change of desert locusts (1). Therefore, the function of different neurotransmitters in the brain and thoracic ganglia needs further investigation.

6. JUMP AND FLIGHT

Locusts jump to escape danger or initiate flight by employing a catapult mechanism (4). Solitary and gregarious locusts perform differently for both a single jump and continuous jumping (100, 153). Solitary locusts jump faster and longer than gregarious locusts due to the increased muscular volume and cuticular specializations of their hind legs (100). On the other hand, gregarious locusts perform better in endurance jumping with a higher frequency of jumps, as well as jumping for longer distances, than solitary locusts (155). The trade-off between maximizing jump velocity in the solitary phase and the ability to quickly and repeatedly jump in gregarious locusts is due to the divergence between using jumping to escape from predators and as a primary means of locomotion, respectively.

Gregarious adults can fly continuously for approximately 12 h, whereas solitary adults are only capable of short-term flight to find mates or food or to escape from predators (89). The plasticity of flight capacity in gregarious and solitary locusts can be qualified and quantified by using comprehensive evaluation involving behavioral, physiological, and multiomics approaches (24). Solitary locusts possess high initial flight speeds for short-term flight, whereas gregarious locusts can fly for a longer distance at a relatively lower speed. Solitary locusts have more active flight muscle energy metabolism than gregarious locusts, whereas gregarious locusts show less reactive oxygen species (ROS) production during flight. The density-dependent flight traits of locusts were attributed to the plasticity of energy metabolism and the degree of oxidative stress production, but not to energy storage (24).

ROS: reactive oxygen species

Hypoxia inducible factor 1 (Hif-1): an evolutionarily conserved transcription factor that plays crucial roles in the cellular and physiological responses to hypoxia

Redox balancing and lipid utilization simultaneously contribute to the long-term flight of gregarious locusts (23, 50). The regulation of hypoxia inducible factor-1 (Hif-1) activity is the focus of hypoxia-responsive gene expression. Hif-1α1 and Hif-1α2, two Hif-1α splice variants, have been identified in the migratory locust. The ubiquitously expressed Hif-1α1, which plays a conserved role in hypoxia adaptation in many other animals (101), remains inactive during flight, a process that is completely aerobic. In contrast, Hif-1α2, which lacks a C-terminal transactivation domain, does not induce canonical hypoxic responses, but instead contributes to flight endurance by maintaining redox homeostasis through increasing production of Dj-1, an ROS quencher (23). These findings reveal a novel function of Hif-1 in prolonged aerobic physiological activity and the importance of redox homeostasis in locust long-term flight.

Adipokinetic hormone/corazonin-related peptide (ACP) has been identified as a key factor in facilitating muscle lipid utilization during long-term flight in locusts. Knockout of *ACP* significantly reduces the prolonged flight ability of locusts and downregulates the genes and metabolites involved in fatty acid transport and oxidation in the flight muscle. The fatty-acid-binding protein (FABP), a downstream factor of ACP, mediates the effects of ACP on lipid oxidation and prolonged flight (50). The significant role of FABP in prolonged flight has also been reported in the desert locust (92), indicating that FABP plays a conserved role in lipid metabolism and long-term flight in two locust species. Moreover, *ACP* knockout significantly alters the contents of multiple lipids in the fat body, demonstrating the crucial role of ACP in maintaining lipid metabolism homeostasis in locusts (51).

7. REPRODUCTION AND AGING

Reproductive success is a key determinant of evolutionary fitness. Solitary and gregarious locusts employ distinct reproductive strategies to adapt to their respective environmental conditions. Solitary males invest more in precopulatory courtship and signaling compared to their gregarious counterparts, although they share similar behavioral elements from the initial encounter to copulation (29, 30). Solitary females less frequently exhibit rejection-related behavioral patterns, increasing the likelihood of successful mating for both solitary and gregarious males (29). On the other hand, desert locusts in dense populations dedicate resources to reducing the costs of male mating harassment. In the lekking sites, once a male mounted a gravid female, the mating pairs were not attacked during the vulnerable time of oviposition (78). The sex-biased behavioral traits in the two phases of locusts may enhance reproduction success at low population density and minimize the costs of male mating harassment and competition at high population density.

Parental experiences in different population densities can affect the phenotypes of offspring. The isolation of gregarious female or male adults can reduce the egg weights and alter the morphometric traits of offspring, while the crowding of the solitary female or male adults exhibits opposite results. In addition, the variation in parental expressions of heat-shock protein genes (*Hsps*) such as *Hsp90*, *Hsp70*, and *Hsp20.6* can also be transmitted to the offspring, and the pattern of inheritance is consistent with that of phase characteristics. Although the effects of population density on the phase state of progeny can be transmitted by both maternal and paternal inheritance, the expression of paternal effects was not as pronounced as that of maternal effects (8). The phase-dependent differences appear in sperm accumulation of the male adult seminal vesicle (48) and reproductive organ development (49), suggesting differential fecundities between male adults of the two phases, but no further functional verifications have been performed. Gregarious female adults exhibit faster and more synchronous sexual maturation compared with solitary locusts (10, 11), and the egg-hatching time of gregarious locusts is more uniform compared with solitary locusts (45). High expression of miR-276 in both the ovaries and eggs promotes synchronous hatching of progeny eggs through upregulation of a transcription coactivator gene, *brahma* (45). The eggs need to be placed in contact with each other to achieve synchronous hatching, and direct mechanical stimulation elicits synchronous hatching among adjacent eggs (83, 102). These traits of gregarious locusts facilitate the formation of swarms and the transgenerational accumulation of gregarious traits.

Oosorption: oocyte resorption, a process by which oocytes stop yolk deposition and are resorbed, decreasing the number of matured oocytes for egg production

Allocation of reproductive resources between egg size and egg number is also an important trade-off strategy that differs between gregarious and solitary locusts. Generally, gregarious locusts produce fewer and larger-sized eggs, while solitary locusts deposit more and smaller-sized eggs (11, 74). In the migratory locust, gregarious oocytes display a 15% higher oosorption ratio than those of solitary locusts. *Activinβ*, targeted by miR-34, mediates the higher oosorption ratio in gregarious locusts (154). On the other hand, solitary locusts increase fecundity by enhancing the frequency of egg laying and clutch size (number of eggs per egg pod) (47, 75). Mechanically, the Piwi protein Liwi1 and piRNAs are highly expressed in early developing egg chambers in solitary locusts and facilitate the upregulated expression of oocyte development–related genes in the germline by enhancing premRNA splicing (47). The increased egg size of gregarious desert locusts is mediated by increasing the oogenesis period and oosorption rate (76). Large eggs have more yolk and space, resulting in larger final embryos than small eggs. The amount of yolk and the size of eggshells during katatrepsis play key roles in determining hatchling body size in desert locusts (77).

Gregarious adult locusts have a shorter lifespan to conserve resources for progeny, while solitary locusts live longer under consistent rearing conditions (2), suggesting a variation in aging rates between these two phases. The aging of desert locusts (*S. gregaria*) is accompanied by a decline in hearing ability (31), an increased diversity of gut microbiota (22), and a slow rate of thickening of the tibia (85). In the migratory locust, the flight performance and sperm state display clear aging-related decline in male adults. The organ-specific aging transcriptional features are characterized by dramatic expression changes in the flight muscle and fat body but minimal changes in the brain. Expression changes in mitochondrion-related genes and detoxification and phagocytosis genes contribute to the predominant transcriptional characteristics of flight muscle and fat body aging, respectively (37). The aging features of flight muscles between solitary and gregarious locusts were further explored in subsequent research. Gregarious locusts display faster locomotor deficits and increased muscle degeneration in aging than solitary locusts. The aging-related flight impairments in gregarious locusts are attributed to the upregulation of *PLIN2*, inducing the accumulation of ectopic lipid droplets and triacylglycerols in flight muscles. The ectopic lipid accumulation leads to a decline in aging-related β-oxidation by restricting fatty acid transport and content (35).

8. INTERACTIONS WITH MICROORGANISMS

The application of the entomopathogenic fungus *Metarhizium* has become an important alternative to chemical pesticides in the control of grasshoppers and locusts (69, 148). However, the improvement of the insecticidal effects of pathogenic fungi is a great challenge. Gregarious locusts display higher resistance to fungus pathogen infections compared to solitary locusts (135, 141). Prophylactically high expression of GNBP3 mediates enhanced humoral immune responses upon *Metarhizium anisopliae* infection (135). In contrast, the hemocytes of gregarious locusts exhibit lower phagocytic ability than those of solitary locusts (134). Gregarious locusts possess high expression of effectors (*gnbp1* and *dfp*), while solitary locusts show high expression of cytokines (*eater* and *tnf*). The higher expression of *tnf* represses the expression of effectors and impairs locust defense against infection with *M. anisopliae* (134). Enhanced humoral defense and reduced cellular defense facilitate the protection of gregarious locusts against the high infection probability of fungus pathogens. To address this issue, researchers have enhanced the virulence of *Metarhizium* fungi by genetically modifying them to accumulate tyramine and express glycerate kinase (119, 120).

The gut microbiota has been suggested to play a role in the locust phase change by microtome sequencing results and mathematical prediction. Several genera, such as *Enterobacter* (Proteobacteria), *Enterococcus* (Firmicutes), and *Weissella* (Firmicutes), show different relative abundance in the hindgut of gregarious and solitary locusts (55). The integument and gut bacteria composition of solitary locusts can be altered after crowding treatment (62). Although the inducing effects of the microbiome were predicted by a mathematical model (61), the functions and mechanisms of microbiota in locust phase change need to be further investigated.

The microsporidian parasite *Paranosema locustae*, which causes severe disease, is also involved in behavioral and morphological phase changes via affecting hindgut bacteria and modulating neurotransmitters such as serotonin, dopamine, and taurine (26, 64, 103). However, the molecular mechanism involved in interactions between this parasite and phase-related phenotypes still needs to be investigated.

9. REGULATORY NETWORK

9.1. Chromatin Modification

The phase changes in locusts exhibit clear epigenetic features. The existence of DNA methylation has been confirmed previously in migratory and desert locusts through methylated cytidine quantification, DNA methyltransferase gene identification, and genome-scale bisulfite sequencing (2, 25, 94). Subsequent research further linked DNA methylation with the locust phase change. Crowd-reared and solitary-reared locusts show dramatically different neural DNA methylation fingerprints, as demonstrated through analysis of methylation-sensitive amplified fragment length polymorphisms (79). The alternative phase states are also associated with significant differences in the expression of the genes *DNA methyltransferase 1*, *DNA methyltransferase 2*, and *methyl-CpG-binding domain protein 2/3* (95). In a study analyzing the embryonic methylation profiles of several intragenic regions and a long interspersed nuclear element (LINE), LmI (a high-copy-number long interspersed nuclear element) and three coding genes (*adenyl cyclase-associated binding protein 2*, *choline kinase alpha-like* and *henna*) were shown to be methylated (95). DNA methyltransferase 3 (*Dnmt3*) expression also shows differential patterns between gregarious and solitary locusts and significantly responds to changes in population density. *Dnmt3* knockdown significantly reduces the phase-related locomotor activity in gregarious and crowded solitary locusts by upregulating genes related to metabolism, transporting activity, and oxidative stress response (54). These findings provide direct evidence that DNA methylation is involved in the locust phase change.

The locust genome encodes a diverse array of histone-modifying enzymes, suggesting that various functional histone modifications exists in the migratory locust (36). Several histone deacetylases and H3K4-specific methyltransferases show different expression patterns in the brains of solitary and gregarious locusts (36). An arthropod-specific gene, *SmydA-2*, has been identified as a new histone modifier possessing histone methylation activity and involved in locust survival through comparative analysis of members of the SET domain-domain containing genes family (SET genes) from 147 arthropod genomes and experimental verification (57). These studies revealed the primary characteristics of histone-modifying enzymes and offer crucial insights into the role of histone modifications underlying locust polyphenism.

9.2. Transcriptional and Post-Transcriptional Regulation

RNA *N*6-methyladenosine (m^{6}A): an RNA modification regulating gene expression at the post-transcriptional level and directly affecting protein production

The processes of locust phase change are involved in transcriptional and post-transcriptional regulation, as described above. In fact, the regulation is not limited to a single gene or pathway; it is more likely to be networked. A large number of high-throughput transcriptome data sets have been continuously gathered from various developmental stages, tissues, and time courses of the phase transition in the migratory locust (8, 12, 131, 135, 144). Through a comprehensive analysis of multiple phase-related transcriptomic data sets of the migratory locust, PhaseCore genes have been defined according to their contributions to phase differentiation. These PhaseCore genes can accurately predict phase status with over 87.5% accuracy and exhibit unique gene attributes, such as faster evolution rates, higher CpG content, and higher specific expression levels. Three representative TFs (Hr4, Hr46, and grh) among the 20 identified PhaseCoreTF genes have been verified to play critical roles in locust phase transition (147). Studies of these TFs revealed that core transcriptional signatures play a key role in regulating locust phase changes. Other research performed a meta-analysis using the published RNA sequencing data of aphids and locusts to reveal the DEGs in response to crowded and isolated conditions (118). The results indicated that DNA replication, DNA metabolic processes, and the mitotic cell cycle significantly respond to crowded conditions, while the oxidative stress response and neurological system modifications are highlighted under isolated conditions (118). These processes are believed to play critical roles in the regulation of density-dependent plasticity, but direct functional verification is required in future studies.

Changes in gene expression in response to environmental changes have been substantially reported in insect phenotypic plasticity, such as the transition between summer-form and winter-form morphotypes of *Cacopsylla chinensis* (149), the caste-specific behavior of *Camponotus floridanus* (104), and the worker-gamergate transition of *Harpegnathos saltator* (32), among others. Although the key genes and mechanisms varied in different model system, changes in the expressions of these genes are always significantly correlated to the change of phenotypes. Thus, the transcriptional signatures driven by certain key TFs in response to environmental changes are potential conserved mechanisms in the phenotypic plasticity of insects.

Small RNAs are important regulators in post-transcriptional modification. In recent years, research on small RNAs in locusts has progressed from prediction, identification, and comparison between two phases (133, 136, 140, 152) to global screening and functional verification of key small RNAs related to specific phenotypes or pathways during the phase change. miRNAs (e.g., miR-133, miR-9a, miR-8–5p, miR-276, miR-71, and miR-263) and piRNAs (e.g., piRs-3-I2+I3 and *Orb*-related piRs), as well as multiple gene targets, have been confirmed to play crucial roles in various aspects of the locust phase transition, such as behavioral change, egg-hatching synchrony, molting, food intake, and fecundity (41, 45–47, 130, 145, 146).

One study applied high-throughput RNA-sequencing to compare the expression patterns of lncRNAs and mRNAs during the locust phase transition and demonstrated that lncRNAs respond more rapidly in the early stages of the phase transition. The early changed lncRNAs utilize distinct pathways to adapt to changes in population density (66).

The most abundant modification of mRNA, RNA *N*6-methyladenosine (m^{6}A), has been verified to play crucial roles in the phase change of the migratory locust. The methyltransferase genes (*METTL3 and METTL14*) and the demethylase gene (*ALKBH5*), which are key in m^{6}A modification, exhibit remarkable expression patterns responding to density changes in the brain and regulate gregarious and solitary behavior, respectively. RNAi knockdown of *ALKBH5* induced more than 3,000 DEGs, and m^{6}A immunoprecipitation sequencing revealed that hundreds of genes exhibited significant m^{6}A modifications. Among them, *Lim3*, a transcription factor controlled by m^{6}A modification, was verified to regulate the locust behavioral phase change.

Global m^6A modification contributes to the orchestration of gene expression, fine-tuning the behavioral change of locusts (56).

Epigenome: the entire array of gene expression states imposed by chromatin and nonhistone regulators on the genome

A phase-dependent pattern at the translation level, with distinct polysome profiles between gregarious and solitary locusts, has been found (65). In gregarious locusts, 10 genes associated with the cytosolic ribosome pathway show increased translational efficiency (TE), while in solitary locusts, 5 genes involved in the mitochondrial ribosome pathway exhibit increased TE. The accumulation of the free 60S ribosomal subunit and the elevated assembly of mitochondrial ribosomes contribute to the divergence of the translational profile and behavioral change between gregarious and solitary locusts (65). This study sheds light on the molecular mechanisms underlying locust phase transition, from transcriptional levels to translational levels.

10. CONCLUSIONS AND PERSPECTIVES

In recent years, the genome assemblies of the migratory locust, *L. migratoria* (131), and the desert locust, *S. gregaria* (128), have dramatically promoted the progress of research on locust polyphenism. The regulation of locust phase change is networked, encompassing the full-chain regulation from genes to transcriptional, post-transcriptional, translational, and epigenetic regulation. The high-quality chromosomal-level genomes and epigenomes of locusts, the global and precise orchestration of gene expression, mRNA alternative splicing, and various modifications at multiple levels will be beneficial for in-depth study of the molecular mechanisms underlying locust phase change. Additionally, gene manipulations through RNAi and CRISPR-Cas9 have been widely utilized in locusts. Although gene downregulation can be easily achieved by these approaches, the overexpression of endogenous genes and insertion of exogenous genes were not reported until recently. Reverse genetics through CRISPR-Cas9-mediated gene manipulation will potentially introduce more phenotypes related to locust adaptation strategies.

Numerous research efforts have demonstrated that the dopamine pathway is a core regulatory factor in the phase change of the migratory locust. From the metabolism to signaling, dopamine and its synthesis enzymes play pivotal roles in regulating behaviors at multiple levels. lncRNA and miRNA mediate the transcriptional and post-transcriptional regulation of key biosynthetic enzyme expressions, and dopamine receptor–elicited cascade signal transduction constructs the multifaceted regulatory network and facilitates the accurate regulation of the locust phase change. As dopamine acts in the migratory locust brain, dopamine and its synthesis enzymes serve as an important biological basis in regulating behavioral and olfactory responses when the population density fluctuates.

One interesting discovery is the special metabolism of phenylalanine in locust phase changes (**Figure 2**). Dopamine biosynthesis is closely related to phenylalanine, an essential amino acid that can only be obtained from dietary sources (28). Massive key modulators of the locust phase change are directly or indirectly correlated with phenylalanine. The biosynthesis of key biogenic amine neurotransmitters (dopamine, octopamine, and tyramine, for instance) and key pheromones (PAN and 4VA, for instance) can all be traced back to phenylalanine metabolism. Phenylalanine can be converted to tyrosine by phenylalanine hydroxylase (*henna* or *PAH*), and dopamine, tyramine, and octopamine are all derivatives of this pathway (70, 129, 150). Tyrosine hydroxylase (*pale*) catalyzes the conversion of tyrosine to L-DOPA, and L-DOPA is decarboxylated by aromatic amino acid decarboxylase (*Ddc*) to generate dopamine (18, 70). Tyramine is transformed from tyrosine by tyrosine decarboxylase and then converted to octopamine by tyramine β-hydroxylase (68, 80). Phenylalanine is also the precursor of the aposematic pheromone PAN and the aggregation pheromone 4VA. A key enzyme, CYP305M2, catalyzes the transformation of phenylalanine to (Z)-PAOx and is a rapid-limiting enzyme of PAN biosynthesis in locusts (138). Recently, the biosynthesis of the aggregation pheromone 4VA has been conformed to start from phenylalanine.

Aromatic compounds occupy a large proportion of the pheromone profiles of locusts (44, 139), and their similar structure suggests these compounds are probably related to phenylalanine. Phenylalanine acts as the substrate of lignin and is widespread in most plants (3). Thus, locusts can conveniently obtain this compound and produce various modulators through brief modification or transformation. These processes allow locusts to effectively respond to changed environments. Therefore, we propose that locusts transfer their phase states through alterations in the metabolism of phenylalanine linked with density changes.

The trade-off between long-distance migration and local reproduction is of great importance for locust survival and evolution. After 100 years of research on locust phase changes, we are able to conclude that most aspects of the phase transition of locusts serve to facilitate the trade-off between migration and reproduction. Gregarious locusts have to face the great challenges of resource shortage and fierce competition due to the high density within swarms. Consequently, the gregarious locusts manage to obtain more resources through group living, marching, and long-distance migration, while the solitary locusts prioritize procreation. The gregarious locusts specifically produce 4VA for aggregation, whereas the solitary locusts emit more sexual pheromones for partner searching. The black-brown pattern and PAN in gregarious locusts facilitate the warning of and defense against natural predators, whereas the solitary locusts utilize green coloration as camouflage. The solitary locusts exhibit high-velocity flight for escaping from natural predators, and the gregarious locusts can sustainably fly at relatively moderate speeds to search for food and reproduction resources during long-distance flights. The gregarious locusts exhibit a relatively faster aging rate than that in solitary locusts to facilitate the reduction of futile food consumption and the increase of nutrient availability for progeny. On the other hand, with cryptic living habits and adequate food supply, the long lifespan in solitary locusts will enhance the chance of copulation and egg laying. Taken together, the gregarious and solitary locusts employ different survival strategies in response to their respective environments during their entire life cycles. Hence, over a long historical period, the conversable transition between the solitary and gregarious phase is mutually dependent, primarily influenced by the local population density at a given temporospatial condition.

The identified key modulators involved in the transition from the solitary to gregarious phase and the transfer of gregarious traits to the next generation pave the way for the sustainable prevention of locust plagues in the future. Development of novel powerful regulating reagents to manipulate the key behavioral regulators, such as neurotransmitters, neuropeptides, miRNAs, piRNAs, and lncRNAs, is an effective control measure for the occurrence of locust swarms. Additionally, interactions among locusts and symbiotic microbiomes or fungus pathogens will open a new path to understanding locust phenotypic plasticity, as well as to being able to use biocontrol agents more effectively. The investigation and modification of virulence factors from fungus pathogens will lead to the development of novel biopesticides, which can be used to control not only locusts, but also other pests. On the other hand, at a large scale, climate change, such as changes in temperature, wind, and rainfall, can influence insect polyphenism by altering biotic and abiotic cues (93). Consequently, monitoring and predicting locust population changes based on large-scale spatial and temporal data can also be effective macrocontrol measures.

SUMMARY POINTS

1. Locusts exhibit remarkable phenotypic plasticity in response to population density changes, displaying phenotypes that are distinct between the solitary and gregarious phases.

2. The dopamine pathway is a core regulatory factor in the behavioral phase change of locusts.
3. Key modulators of locust phase change, such as dopamine, octopamine, tyramine, PAN, and 4VA, are directly or indirectly correlated with phenylalanine.
4. The regulation of the locust phase change is networked, encompassing the full chain of regulation from genes to the transcriptional, post-transcriptional, translational, and protein modification levels.
5. Most aspects of the phase transition of locusts serve to facilitate the trade-off between long-distance migration and local reproduction.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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