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Research Article

Phenotypic plasticity in grasshoppers and locusts: a review

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Abstract:

Phenotypic plasticity is a crucial adaptation mechanism in the animal kingdom, where a single genotype can modify its outward features in response to stimuli from the outside. Changes in shape, behaviour, and life history features are just a few ways in which phenotypic plasticity can be observed in insects. Body size, wing length, and colouration are examples of how morphology can alter in reaction to environmental factors. This phenomenon allows animals, especially insects, to modify their physical characteristics, behavioural patterns, and life history features in response to environmental stimuli. This article addresses the phenotypic plasticity observed in locusts and grasshoppers, highlighting their impressive ability to alter morphological, physiological, and behavioural traits in response to environmental changes. This review seeks to establish a fundamental comprehension of the mechanisms that govern phenotypic plasticity in grasshoppers and locusts, with the goal of laying the baseline for future scientific investigations into this novel phenomenon.

Keywords: Phenotypic plasticity, Insects, Grasshoppers, Animal behaviour, Insect behaviour, Adaptation mechanism, Insect behavioural pattern, Environmental stimuli.

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1. Introduction

An alteration in the phenotype that is exhibited by a genotype as a result of the environment, or the phenomenon that occurs when the environment changes the phenotype of an individual, is regarded as phenotypic plasticity (Scheiner, 1993). According to Agrawal (2001), the capacity of an organism to exhibit a variety of phenotypes in response to its surroundings is known as phenotypic plasticity. The term "phenotypic plasticity" describes how a single genotype can change its outward appearance in reaction to external stimuli. Phenotypic plasticity allows animals to change their appearance, behaviour, or life history characteristics in response to their surroundings. Insects are just one of many creatures that exhibit this typical natural occurrence. Organisms can improve their chances of survival and reproduction by modifying their phenotype in response to shifting environmental conditions (Moczek, 2010). Changes in shape, behaviour, and life history features are just a few ways in which phenotypic plasticity can be observed in insects. Here are a few instances where insects have shown phenotypic plasticity: body size, wing length, and colouration are just a few examples of how morphology can alter in reaction to environmental factors. Behaviour changes include various ways of finding food or how they mate in different places. Changes in social insects' life history traits, including reproductive tactics, developmental rates, and caste determination (Shingleton *et al.*, 2007; Lindstrom *et al.*, 2001; Sword, 2002; Emlen & Nijhout, 2000; Day *et al*., 2003).

2. Purpose and scope of the review

A literature review on phenotypic plasticity could aim to cover a wide range of topics and cover multiple objectives: The purpose of this review is to compile and summarize what is currently known about phenotypic plasticity from a variety of sources, including different types of animals, habitats, and academic fields. It has the potential to give a thorough synopsis of phenotypic plasticity-related processes, ecological relevance, evolutionary consequences, and research methods. A review can find commonalities and patterns in the field of phenotypic plasticity by reviewing a variety of studies and research results. The variables that impact plastic responses, plasticity's adaptive significance, and the ecological and evolutionary effects of phenotypic flexibility can be better understood with this information. Third, the methodologies used to study plastic responses in different creatures and environments can be assessed by reviewing phenotypic plasticity. Future research on phenotypic plasticity would benefit from critically evaluating the many approaches taken thus far, including experimental designs, field investigations, and theoretical models. Phenotypic plasticity research is dynamic; new questions and focus areas arise frequently. A review is a great way to delve into fresh debates, issues, and arguments in the field while also drawing attention to underexplored areas. By critically evaluating relevant literature and identifying knowledge gaps, a review of phenotypic plasticity can help motivate and prioritize future research. A better understanding of phenotypic plasticity in many biological environments can be advanced by developing new hypotheses, experimental approaches, and interdisciplinary collaborations.

3. Systematic review of phenotypic plasticity in grasshoppers and locusts

3.1. Role and benefits of phenotypic plasticity

Phenotypic plasticity relies heavily on physiological processes that mediate the organism's response to environmental signals. These processes, which include a wide range of physiological levels and systems, help the organism adjust to new environments. For instance, physiological pathways and processes support adaptive responses like pathogen-induced plasticity, body size and allometry alterations, wing polyphenisms, stress protein synthesis, and social caste determination in insects. To fully grasp how phenotypic plasticity works, one must be familiar with the physiological and biochemical mechanisms that underlie these adaptive responses (Shingleton *et al.*, 2007; Whitman & Agrawal. 2009).

Microarrays, including gene expression surveillance, are two examples of the modern molecular technologies that have helped scientists uncover the precise genes and pathways that underlie phenotypic plasticity and the adaptive responses it entails. Research is currently underway that is helping to clarify the complex physiological processes that allow insects and other species to exhibit such amazing phenotypic flexibility (Frankino & Raff, 2004; Lessells, 2006; Murren *et al.*, 2015; Kokubun *et al.*, 2016).

Insect phenotypic plasticity benefits include adaptability, physical activity, novelty, and evolution. Insects may adapt their phenotypic to environmental changes, such as temperature and moisture fluctuations, allowing them to adapt to diversity and unpredictability. Phenotypic plasticity can help organisms survive and reproduce in diverse habitats, providing a fitness advantage. It also provides insight into insect species' evolutionary and ecological adaption to drastically changing climates (Tétard-Jones *et al.*, 2011).

3.2. Key factors and importance of phenotypic plasticity in insects and grasshopper

Several essential elements affect phenotypic plasticity's adaptive value: The adaptive utility of phenotypic plasticity can be influenced by the degree of environmental variability and predictability. The capacity to alter phenotypes in reaction to environmental changes could prove useful for creatures existing in highly varied or unpredictable environments. The foundational physiological processes and mechanisms determine the utility of phenotypic plasticity for adaptation. A thorough understanding of the underlying biochemical and physiological processes is necessary to determine reactions' adaptive significance. Phenotypic plasticity's adaptive value hinges on its effects on fitness, which encompasses development, procreation, and longevity. Plastic reactions that boost fitness in specific contexts are likely adaptive. The evolutionary background and selection pressures experienced by a species might impact the adaptive significance of phenotypic flexibility. Evolutionary processes can shape the adaptive significance of plasticity, and there are situations in which plasticity might be more advantageous (Hess *et al.*, 2022).

Locusts are a type of grasshopper that belongs to the family Acrididae. They have the ability to form large swarms that migrate together. This behaviour results from a phenomenon called density-dependent phenotypic plasticity, where individual locusts can change their appearance and behaviour in response to increases in population density. Initially, locusts are cryptically coloured and shy, but as the population density rises, they transform into conspicuously coloured and gregarious individuals. These insects undergo various changes in their physical characteristics, reproduction, development, physiology, biochemistry, molecular composition, and ecological interactions, influenced by population density. Locusts exhibit polyphenism in response to variations in local population density, displaying two distinct phenotypes defined as the solitarious and gregarious phases. The phenomenon of synchronised alterations is referred to as locust phase polyphenism (Song *et al.*, 2017; Whitman & Ananthakrishnan, 2009;

Pener & Yerushalmi, 1998). Phenotypic plasticity is crucial for grasshoppers and insects because it allows them to show diverse phenotypes in response to environmental signals. To summarise, phenotypic plasticity is very essential in grasshoppers and insects.

Insects and grasshoppers have the remarkable ability to adjust to ever-changing environments. They can increase their chances of survival and reproduction by adapting their look, behaviour, and life history traits to thrive in specific situations through phenotypic plasticity. Grasshoppers and insects, for example, can alter their appearance to blend in with their surroundings; this adaptation impacts their social interactions. Adaptations in size or colouration in response to predators can alter predation vulnerability; changes in behaviour can alter feeding strategies and interactions with competitors, affecting behaviour. Phenotypic flexibility can impact the evolutionary routes of grasshoppers and insects as a means of rapid adaptation to new habitats. Some phenotypes can evolve into adaptive ones because natural selection favours plastic responses that boost fitness in specific environments. Learning more about the phenotypic plasticity of grasshoppers and insects can help researchers and conservationists comprehend their ecology, physiology, and evolutionary biology. Understanding how these organisms respond to environmental changes can help in the preservation of biodiversity and the functioning of ecosystems. Insights gained from this study might inform conservation efforts and management strategies (DeAngelis & Mooij, 2005; Swallow *et al.*, 2005; Gardner & Agrawal, 2002; Beckerman *et al.*, 2002; Agrawal, 2005; Werner & Peacor, 2003).

Locusts demonstrate a remarkable instance of complex phenotypic plasticity in nature, where variations in population density led to the transformation of solitary and inconspicuous individuals into social and noticeable locusts that form vast travelling swarms. They conducted a study to examine the evolutionary origins of coordinated alternative phenotypes by analysing the Central American locust and three closely related non-swarming grasshoppers comparatively. An experiment resulted in isolated and crowded nymphs during their growth. This caused them to exhibit density-dependent phenotypic plasticity. They measured the consequent changes in their behaviour, morphology, and chemical reaction norms (Fouquet *et al.*, 2021).

3.3. Evolutionary consequences of phenotypic plasticity

Among the several evolutionary consequences of this phenomenon is the significance of phenotypic plasticity in adaptation, genetic diversity, and the formation of novel phenotypes. Some of the most significant evolutionary effects of phenotypic plasticity include Phenotypic plasticity (the ability to alter one's phenotype in response to environmental changes temporarily), which allows animals to adapt to their environments very quickly. Sustaining one's species and passing it on to future generations depends on one's adaptability to novel and ever-changing environments. The ability for diverse phenotypes to be displayed in different situations is a critical component of phenotypic plasticity, ultimately maintaining variation in genes within populations. This diversity can provide the building blocks for natural selection, boosting a species' chances of evolution in the long run. The Derivation of New Characteristics: In reaction to specific environmental signals, phenotypic plasticity can cause the emergence of new phenotypes. After these new characteristics have taken root, they can be assimilated into a population's DNA through mechanisms like genetic assimilation, which could lead to evolutionary innovation. Fourthly, phenotypic plasticity can affect evolutionary trajectories, meaning the way and how fast a population or species evolves. Natural selection can alter population genetic makeup through time by influencing plastic responses that improve fitness in particular habitats (Schlichting, 2004; Price, 2006; Suzuki & Nijhout, 2006)

3.4. Life history and ecology of grasshoppers and locusts

Life cycles, ecology, behaviour, and the interplay between grasshoppers and locusts and their environments encompass various fascinating subjects. The species' ecological and biological characteristics are outlined in critical points below: Attributes Throughout Life: The life cycles of grasshoppers and locusts exhibit a broad variety of traits, including the ways in which they lay eggs, the stages of development (egg, nymph, adult), the reproductive strategies they employ, and the duration of their lifespan. A thorough understanding of the life cycles of insects allows for improved prediction of their population dynamics and responses to alterations in their natural environment. Grasshoppers and locusts can be found in various habitats, including grasslands, meadows, agricultural regions, and deserts. Their distribution is influenced by factors such as food accessibility, temperature, and humidity. Migratory behaviour is a response of some animals to changes in their surroundings. Since they are herbivores, grasshoppers and locusts can be found eating a broad variety of plants. Because of the influence they have on agricultural crops and plant communities through their diet, they are vital to ecosystems. Grasshoppers and locusts use a variety of reproductive tactics, such as mate selection, wooing behaviour, and oviposition site selection, to control pest outbreaks and preserve biodiversity. Different animals respond to their environments by either being solitary or social, and some have intricate mating systems. Grasshopper and locust populations can experience sudden shifts in reaction to changes in their environment, which can cause outbreaks or population collapses. Reproductive success is affected by factors including resource availability and population density. There are several variables that might influence population dynamics, including the amount of predation, temperature, humidity, and the availability of food. Understanding the factors influencing population growth is vital for conservation and pest control efforts (Song, 2005; Stearns, 1998; Steigenga & Fischer, 2007; Stern, 1994; Strauss & Irwin. 2004; Sugumaran, 2002).

3.5. Environmental factors that affect grasshopper and locust communities

A variety of natural factors influence grasshopper and locust ranges and habitats. The following are some of the most essential natural variables affecting grasshopper and locust ecosystems. Grasshoppers and locusts regulate their internal temperature based on their surroundings. Temperature influences their growth, development, and metabolism, all of which have an impact on their distribution and abundance. Temperature tolerance varies by species; some are more adapted to specific ranges than others. Another important environmental factor influencing grasshopper and locust habitats is dampness. These insects seek food and shelter in vegetation that thrives in high-humidity locations, which promotes their growth. Diseases like fungal infections may impair their capacity to survive and multiply if humidity levels are too high. Plants provide nutrition and protection for herbivores, grasshoppers, and locusts. The type and quantity of vegetation can influence their distribution and abundance in a specific area. Some species have evolved to graze only on specific types of plants, while others may ingest a wide variety of vegetation. The quantity of moisture in the earth's surface considerably impacts plant growth and maintenance, which in turn influences the habitats in which grasshoppers and locusts thrive. Some species require damp soil for oviposition, whereas others can thrive on dry soil. Many diverse mammals, birds, and insects eat grasshoppers and locusts. Predation forces can impact these organisms' range, abundance, behaviour, and reproduction techniques. Some animals use gregarious behaviour as a defence mechanism, whereas others rely on camouflage or adaptations. Human activities such as land use change, agriculture, and urbanisation can all have an impact on grasshopper and locust habitats. These insects are susceptible to variations in moisture in the soil, cover of plants, and other ecological factors caused by human activities such as habitat division and pesticide use.

3.6. Key ecological roles of grasshoppers and locusts

Because of their relationships with plants, predatory animals, and other creatures, grasshoppers and locusts serve significant ecological functions in diverse environments. Grasshoppers and locusts play an important part in the ecosystem as follows: Grasshoppers and locusts are insect species that primarily consume plants, specifically a diverse array of plants. They can alter plant communities' dynamics, structure, and composition just by eating plant matter. The way they feed has the potential to influence ecosystem productivity, nitrogen cycling, and patterns of vegetation. Many predators, including birds, mammals, reptiles, and other insects, rely on grasshoppers and locusts as a food supply. Moving nutrients and energy from plants to higher trophic levels plays a crucial role in the food web. The dynamics of ecosystems and predator populations are affected by their abundance and where they are distributed. Some species of grasshoppers and locusts help spread seeds to new areas by eating them and then carrying them elsewhere. This can potentially aid in plant diversity maintenance, colonisation of previously uninhabited areas, and plant regeneration. The structure and dynamics of plant communities can be impacted by the distribution of seeds by these insects. Grasshoppers and locusts play a crucial part in the cycling of ecosystem nutrients by feeding and expelling waste. They contribute to soil fertility and nutrient recycling by eating plant matter and then releasing those nutrients back into the soil. Interactions between soil and plants can impact nutrient dynamics in ecosystems. Grasshoppers and locusts, being herbivores, can regulate plant populations. They manage plant development, reproduction, and population density by feeding on plant matter. Their feeding habits can potentially affect community organisation, population dynamics, and plant fitness. In terrestrial ecosystems, grasshoppers and locusts play a significant role in biodiversity. Ecosystems' diversity, abundance, and interconnections make them complex and robust. The ability to understand these insects' ecological functions is critical for insect biodiversity conservation and ecosystem function preservation (Roelofs *et al.*, 2008; Roff, 1996; Rogers & Simpson, 1997; Rountree & Nijhout, 1994; Roy *et al.*, 2006).

3.7. Mechanisms of phenotypic plasticity

Phenotypic plasticity refers to an organism's ability to change its phenotype in response to stimuli or changes in its external environment. Various genetic, growth-oriented and physiological processes may play a role in phenotypic plasticity. Here are several essential ways that phenotypic plasticity works: Developmental plasticity. Developmental plasticity refers to phenotypic changes caused by environmental cues. This category encompasses diversity in development, shape, size, and behaviour. Changing one's phenotype to fit one's environment better is an important aspect of developmental plasticity. Physiological plasticity refers to an organism's ability to adapt to new environmental stimuli. Numerous biological pathways, including metabolic processes, levels of hormones, and enzyme function, may be affected. Organisms' physiological flexibility allows them to adapt to their environments and survive in dynamic conditions. Behavioural plasticity refers to an organism's ability to adjust to new environmental stimuli. Such modifications include feeding, mating, predator avoidance, and social interaction. Genetic plasticity is the gene expression or regulation adjustment in response to environmental stimuli. In contrast, behavioural plasticity allows animals to adapt to changing environmental situations and maximise their chances of survival and reproduction. This category includes epigenetic changes, changes in gene networks, and the up-or-down-regulation of specific genes. Because of genetic plasticity, animals can change their appearance without changing their DNA. Epigenetic systems play an essential role in phenotypic plasticity because they regulate gene expression in response to environmental inputs. This process can include histone modifications, DNA methylation, and non-coding RNA molecules that impact gene activity without changing the DNA sequence. Epigenetic changes, in addition to affecting long-term phenotypic responses to environmental signals, can sometimes be reversed. The control of hormones is a crucial aspect of phenotypic plasticity because it coordinates physiological and developmental responses to environmental inputs. In response to environmental changes, hormones such as insulin-like peptides, ecdysteroids, and juvenile hormones can regulate development, growth, and behaviour. Hormone regulation is essential for coordinating adaptive responses to changing environmental conditions (Shingleton *et al.*, 2007; Amdam *et al.*, 2007; Emlen & Allen, 2003; Emlen *et al.*, 2007).

The phase change in desert locusts is a response to the arid conditions of their habitat, characterised by sporadic and irregular but significant rainfall events. Periods of temporary and plentiful plant growth following heavy rainfall facilitate a rapid rise in the number of solitary locusts. Nevertheless, the supplies are depleted swiftly, resulting in many solitary locusts vying for limited areas of vegetation. The increase in population density leads to increased physical contact among individuals of the same species. It is the continuous presence of this enforced crowding that initiates gregarisation. Crowding significantly impacts behaviour, causing solitarious locusts to adopt critical behavioural traits of the gregarious phase over a short period of 4-8 hours. These traits include heightened activity and movement and a tendency to gather together. The desert locusts' density-dependent polyphenism is seen in the variations in the acquisition of unpleasant associative memories between different phases. The phenomenon of phase change, specifically gregarisation, is crucial in determining the level of reinforcement associated with toxins. Long-term social locusts have the ability to acquire aversions to certain smells through poisonous substances they consume. This, along with peripheral mechanisms, helps them decrease the chances of toxic poisoning and enhance their chances of survival. Pre-existing associative memories are unaffected or interrupted by the process of transitioning into a group formation. The phase-dependent reinforcement value arises from alterations in feeding behaviour that occur due to the phase transition in desert locusts. Therefore, the neuroecology of learning in desert locusts seems to be connected to a change in the antipredator tactic, transitioning from crypsis in solitarious locusts to aposematism in gregarious locusts. In summary, these data illustrate that polyphenism has the ability to generate remarkable disparities and swift alterations in the learning skills among different phenotypes. In addition, the observation that memories can be preserved despite changes in the mechanisms of memory formation during phase transition indicates that the polyphenic procedure can exert a specific, instead of a general, impact on the acquisition processes, even when a creature is undergoing significant behavioural and physiological reorganisation. The learning capacities of each phenotype do not seem to be a result of the phenotypic plasticity but rather are integrated with their specific life history and strategy used to adapt to their varied surroundings (Simoes *et al.*, 2016).

3.8. Plasticity in morphological traits

Phasing plasticity refers to the ability of an organism to alter its morphological characteristics in response to environmental stimuli or changes. Phenotypic plasticity allows organisms to change their sizes, shapes, and phenotypes in response to environmental changes. Regarding morphological characteristic adaptability, the following are some key points: Morphological traits can adapt to environmental signals. Many organisms' body size, appendages length, and overall shape can change due to changes in growth caused by variations in nutrition, climate, or availability of resources. Factors including population density, food availability, humidity, and temperature can set off plastic reactions in morphological features. These signals can potentially affect how an organism's physical traits are formed through the regulation of certain genes, hormone pathways, and developmental processes. Morphological trait plasticity allows organisms to customise their body features for particular environmental circumstances, which is of great adaptive significance. When faced with windy conditions, insects may lengthen their wings; when plants are stressed by drought, they may grow deeper roots. These alterations improve an organism's ability to adapt to different settings. Some morphological plasticities can be undone, but others can stay there for a long time. Organisms can change their physical characteristics in reaction to temporary environmental changes through reversible plasticities. However, they can also undergo more permanent changes in response to changes in their environment over more extended periods. Genomic and epigenetic mechanisms can alter gene expression, cell differentiation, and tissue growth, resulting in phenotypic plasticity. Morphological phenotypic changes can be caused by epigenetic changes and the activation of certain genes in response to environmental inputs. Morphological changes can influence how an organism communicates with its surroundings, how it collects resources, and the overall dynamics of the ecosystem. Changes in the size or shape of an organism, for example, may affect how it contends for assets, prevents predators, or disperses in its ecosystem. Understanding flexibility in morphological traits is critical for understanding how creatures respond to changes in their environment and adapt to various types of habitats. This type of phenotypic plasticity is essential for shaping an organism's physical characteristics and interactions with its natural environment (Agrawal *et al.*, 1999; West-Eberhard, 2003; Pfennig, 2007; Bateson *et al.*, 2004).

4. Challenges and future directions

The issues and potential techniques for understanding phenotypic plasticity entail a wide range of research disciplines and theoretical considerations. Listed below are a few significant challenges and potential paths for success in this field: Understanding the precise genetic, cellular, and physiological mechanisms that suggest phenotypic plasticity remains difficult. Future research may focus on the hormonal, epigenetic, and genetic networks that mediate plastic responses in many features and species. Intricate interactions between developmental and signals from the environment usually characterize phenotypic plasticity. In order to comprehend how animals use complex environmental data to generate adaptable phenotypic reactions, future studies may merge ecology science, biology of development, and ecological science. It is challenging to assess the fitness impacts of phenotypic plasticity in various ecological settings and human populations. In the future, scientists may attempt to quantify how plastic responses influence fitness, population dynamics, evolutionary trajectories, and adaptations. Future studies might concentrate on understanding the methods and extent of transgenerational plasticity, which happens when one generation's environmental experiences influence the phenotypes of another. Understanding the ecological and evolutionary implications of transgenerational plasticity is an essential research topic in this field. Similarly, unravelling the complexities of multi-trait plasticity provides a daunting challenge with the aim of understanding the flexibility displayed by many species across multiple traits at the same time. Future research may focus on the ecological, developmental, and genetic components of coordinated plastic responses across several phenotypic traits. Incorporating knowledge of phenotypic plasticity into conservation and management plans is a promising future direction. Conservation efforts and ecosystem management can benefit from a greater understanding of how plasticity influences climate change responses, invasive species dynamics, and species interactions. Collaborating together in domains such as evolutionary biology, physiological science, the environment, and genetics advances our comprehension of phenotypic plasticity. The complexities of phenotypic plasticity, including its impact on many biological systems, may need future joint study endeavours. To increase our understanding of phenotypic plasticity, its adaptive and environmental significance, and practical applications in biology and environmental science, we need to overcome hurdles and pursue future paths.

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