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Decoding insect diapause: Insights into physiology, environment, and Ecology

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Abstract

Diapause is a hormonally regulated, genetically programmed state of developmental arrest in insects that enables survival during predictable periods of environmental adversity, such as extreme temperatures or food scarcity. Unlike quiescence—which represents an immediate, reversible response to unfavorable conditions—diapause is initiated in advance, often in response to environmental cues such as photoperiod and temperature. This review synthesizes current knowledge on the multifaceted nature of insect diapause, beginning with a conceptual comparison between diapause and quiescence and clarifying its distinctions from other hypothermic states. It explores the environmental signals—particularly photoperiod and temperature—as well as ecological and nutritional cues that trigger diapause, an evolutionary conserved survival strategy in insects. The review outlines embryonic, larval, and pupal diapause, detailing the sequential phases of diapause: preparation, initiation, maintenance, and termination, with emphasis on seasonal forms such as winter and summer diapause. The diversity of diapause strategies across insect taxa and the evolutionary trade-offs they entail are also discussed. Finally, the review examines key physiological and behavioral adaptations, maternal effects, hormonal control mechanisms, and environmental factors that influence the initiation, duration, and termination of diapause in insects. By integrating ecological, physiological, and developmental perspectives, this review provides a comprehensive understanding of the mechanisms and evolutionary significance of diapause in insect life histories.

Keywords: Insect diapause, quiescence, developmental arrest, photoperiodism, environmental cues, hormonal regulation

Introduction

Insects, incredibly diverse and abundant, inhabit nearly every terrestrial and freshwater habitat, including extreme environments like sulfur springs and glaciers [1, 3]. One of the major reasons insects have successfully colonized and thrived in nearly every environment on Earth is their development of various adaptive strategies to cope with conditions that may become temporarily or persistently unfavorable for their activity and development [1-6]. In anticipation of predictable, unfavorable environmental conditions that could threaten their survival, many insect species have evolved a series of metabolic changes that begin well before these harsh conditions set in [3-6]. Dormancy is a general term for any period during which an insect's development and metabolism temporarily slow down in response to environmental or evolutionary pressures, enabling it to survive until favorable conditions return. This state encompasses both quiescence and diapause [3-6].

Diapause is a Genetically Programmed Survival Strategy Against Harsh Conditions

Diapause is a genetically controlled process involving a specific set of gene expression patterns that prepare the insect for extended periods of inactivity. It is a physiological state with very specific onset and termination conditions, often initiated even while the environment remains favorable [3-8]. This adaptation allows insects to stockpile nutrient reserves, halt or significantly slow down development, and increase their tolerance to environmental stressors. This state often continues long after conditions improve, allowing insects to conserve energy and nutrient stores. Diapause, an adaptive strategy that insects use to prepare for unfavorable climate conditions, allows them time to undergo significant physiological adjustments before harsh conditions set in [3-8]. These preparatory adjustments for the upcoming harsh conditions include building up lipid and glycogen stores in the body, depositing cuticular lipids to reduce water loss, suppressing reproductive processes, slowing down metabolic activity, and increasing resistance to low oxygen levels and cold temperatures. In addition, insects may change their color to blend in with winter or dry-season environments, migrate to a more suitable location, or find a safe, sheltered place for hibernation. Diapause is critical for survival in seasonal climates, enabling insects to use resources efficiently, exploit various environmental niches, and colonize temperate and polar areas [3-9].

Unlike migration, which allows insects to escape by moving to a different location, diapause is a key survival strategy for escaping harsh conditions in time, enabling insects to endure unfavorable conditions while staying in the same place [6-8].

Diapause is a dynamic process, unfolding at a much slower pace compared to the rapid developmental changes seen in insects that are not in diapause. While molecular-level activity continues quietly throughout diapause in all species, outwardly, development often seems paused. However, in some cases, visible changes occur in insects undergoing diapause, indicating a significant slowdown in developmental processes rather than a complete halt. For instance, during adult diapause in female *Culex pipiens* mosquitoes, ovarian follicles grow steadily but at an extremely slow rate, taking over 20 weeks to reach a size that non-diapausing females achieve in just three days [5-12].

Insects can enter diapause at different life stages, including the embryonic, larval, pupal, or adult phases. Typically, diapause is a genetically-programmed stage-specific arrest or retardation of development and occurs only once per generation, though there are exceptions [8-12]. For insects with a univoltine life cycle (with one generation per year), diapause is mandatory, occurring in every generation at the same life stage. In most other insects, diapause is facultative, meaning it only happens when necessary; otherwise, generations continue uninterrupted [7-12].

Diapause Versus Quiescence

Quiescence, in contrast to diapause, is a type of dormancy that occurs as an immediate reaction to unfavorable conditions, without any advance preparation. Quiescence is a temporary reaction to short-term unfavorable conditions, like a few days of unexpected cold weather. Unlike diapause, quiescence ends as soon as the environment becomes favorable again [9-12]. Quiescence can happen at any stage of development and allows the insect to pause and resume development and/or activity quickly, repeatedly, and at any life stage when environmental challenges arise. During quiescence, an insect's activity and metabolism slow down, but this state is not controlled by genetic programming. Instead, the insect quickly resumes normal functions as soon as favorable conditions return. For instance, an insect placed in a refrigerator will stop developing and become inactive, but will quickly resume activity when returned to warmer conditions. Similarly, if an insect is deprived of food, it may enter a temporary halted state in development that ends as soon as food becomes available. This ability to quickly enter and exit a dormant state is what sets quiescence apart from diapause [5, 9-12]. Unlike diapause, quiescence does not involve a preparatory phase for storing nutrients and energy-rich molecules or for engaging in behaviors such as seeking shelter during harsh seasons [5, 9-12].

These two forms of developmental arrest - quiescence and diapause - are governed by distinct hormonal mechanisms. In studies on adult female linden bugs *(Pyrrhocoris apterus)*, the corpora allata (CA) glands stop producing the juvenile hormone (JH) required for egg production during both starvation-induced quiescence and diapause. However, when food becomes available, the CA immediately becomes active in starved bugs, while it remains inactive in diapausing bugs [9-12].

Diapause as a Case of Polyphenism

Polyphenism is a type of phenotypic plasticity, refers to discontinuous or discrete phenotypes ("either/or") elicited by the environment. Polyphenism is the phenomenon where a single genotype can produce multiple distinct phenotypes in response to different environmental conditions. This adaptive trait allows organisms to switch between different forms, or "morphs," depending on factors such as temperature, diet, or population density, rather than through genetic changes [3-4, 8-10].

In most cases, diapause represents one of two possible developmental pathways that insects having the same genotype can take, making it a classic example of polyphenism. Insects with identical genotype may either enter diapause or continue development without it, depending on the environmental cues they experience during the season [3-4, 8-11].

Environmental Signals Behind Diapause in Insects

Environmental cues that trigger diapause vary widely and can include drought, lack of moisture or food, extreme temperatures, day length (photoperiod), crowding, and even specific conditions experienced by the mother, such as her diet or age during egg-laying. For many insects, especially those in temperate and arctic regions, shortening day length and dropping temperatures signal the onset of winter and the need to enter diapause. Diapause may occur in completely immobile stages, such as pupae and eggs, or it may occur in highly active stages that involve extensive migrations, such as the adult monarch butterfly, *Danaus plexippus*. In cases where the insect remains active, feeding is reduced, and reproductive development is significantly slowed or halted [7-13].

Distinguishing Diapause from Hypothermic States

There are several terms that should be distinguished from diapause: hibernation, estivation, and daily torpor, all of which are forms of controlled hypothermia. In these states, an animal adjusts its body temperature to align with the surrounding environment within a specific temperature range unique to its species. Hibernation, estivation, and daily torpor are all similar physiological states but differ in timing, season, and duration [5, 9-10].

When an animal allows its body temperature to fall close to the ambient temperature for several days or longer during winter, the process is termed hibernation. Hibernation is a strategy for surviving winter cold, where the metabolic rate is reduced to a minimum, and the animal enters a deep sleep, surviving on food reserves stored in the body during the favorable summer period [4-5]. When this form of controlled hypothermia occurs during summer, it is called estivation. Estivation is the dormancy or sluggishness that occurs in some animals (e.g., snails and hagfish) during hot, dry conditions and typically lasts the length of the dry period or season [4-5, 9-10].

When an animal allows its body temperature to fall close to ambient temperature for only part of each day (generally on many consecutive days), the process is termed daily torpor, which can occur in any season. Daily torpor is a state of adaptive hypothermia used by some animals to conserve energy. In torpor, an animal's body temperature may fall within 1°C of the environmental temperature, which in some cases may be near or even below freezing. All metabolic processes slow down to as little as one-twentieth of the normal rate. A state of torpor can occur during hibernation or when resources are insufficient to maintain body temperature [4-5, 9-10].

Facultative Versus Obligate Diapause

Facultative diapause is a flexible response triggered by specific environmental cues, often received well before the diapause begins. In contrast, obligate diapause is genetically programmed to occur at a particular developmental stage, regardless of the presence of the environmental factors. Insects with obligate diapause typically complete only one generation per year, while those with facultative diapause have the flexibility to produce multiple generations within a season. For example, insects with facultative diapause may go through several non-diapausing generations in the summer and then an overwintering generation that enters diapause [4, 8-11].

Both types of diapause, obligate and facultative, can sometimes be found within the same family, such as the Pentatomidae (stink bugs). Specific trends are also observed in certain groups, such as hymenopteran parasitoids: those that parasitize univoltine hosts usually have obligate diapause, whereas those targeting polyvoltine hosts (with multiple generations per year) typically display facultative diapause [4, 7-11].

How and When Insects Enter Diapause

Insects programmed to diapause pass through successive phases, including prediapause induction and preparation, initiation of diapause, continuing maintenance, termination of diapause, and postdiapause physiology and behavior [7-8, 10, 13].

The term "stage-specific" indicates that the ability to enter diapause is generally limited to a single stage of development in each insect species. While diapause can occur in embryos, larvae, pupae, or adults, for most insect species, only one stage of the life-cycle typically has the capacity for diapause. However, there are exceptions, especially in species facing short growing seasons at high latitudes, where diapause may occur at two stages of development [7-9, 10-13].

For example, northern populations of the spruce budworm (*Choristoneura biennis*) enter diapause as second-instar larvae for their first winter, then again as final-instar larvae in their second winter. Similarly, northern populations of the blow fly (*Calliphora vicina*) can enter diapause both as third-instar larvae and as adults. The bruchid beetle (*Bruchidius dorsalis*) undergoes larval diapause in cooler regions but enters diapause as an adult in warmer areas [7-10].

Despite these examples, most insect species only enter diapause in one developmental stage. This stage-specificity does not apply to quiescence, as insects can enter a quiescent state at any stage of development, although the threshold for entering quiescence may vary across stages [7-11].

In *Aedes* mosquitoes, diapause typically occurs during the embryonic or larval stages. Conversely, most *Culex* species undergo adult diapause. In *Anopheles*, diapause has been reported across multiple stages, including embryonic, larval, and adult. Notably, no mosquito species appears to use the pupal stage for diapause [7-11].

Interestingly, diapause characteristics can vary significantly even within closely related species. For instance, the weevil *Exapion ulicis* undergoes adult diapause and lays eggs in the spring, whereas *Exapion lemovicinum* lays its eggs in the autumn and enters larval diapause to survive the winter. These differing strategies are influenced by the fruiting schedules of their host plants [10-13].

Diapause is a complex, multistep process that cannot be easily bypassed. For example, to induce pupal diapause in flesh flies (genus *Sarcophaga*), several conditions must be met: the fly must be genetically capable of entering diapause, the mother must not have undergone diapause herself, the embryos and larvae must be exposed to short-day conditions, and both larval and post-pupariation temperatures must be cool. If any of these conditions are not fulfilled, diapause may not occur or may occur at a much lower rate [10-14].

Embryonic Diapause

Embryonic diapause is a genetically programmed state where embryonic development either halts completely or slows down significantly. This phenomenon allows a delay between fertilization and the completion of embryonic development. During diapause, embryos begin developing but pause for a period before resuming growth. The duration of this paused development is often variable, offering flexibility in timing [10-15]. Among insects, embryonic diapause is notably observed in crickets, grasshoppers, and walking sticks from the Orthoptera order, true bugs in the Heteroptera order, butterflies and moths within Lepidoptera, and lower Diptera such as mosquitoes and midges. Diapause can occur at nearly any stage of embryogenesis, ranging from the initial formation of the blastoderm to the final stages of pharate larval development, where the fully formed first-instar larva remains unhatched [9, 13-15].

The eggs laid by silkworm moths *(Bombyx)* offer a well-studied example of embryonic diapause in insects. In these eggs, the nature of diapause is influenced by the developmental conditions of the mother. After mating and fertilization, the mother lays eggs programmed to halt their development entirely (stopping mitosis) when they reach the gastrula stage of embryonic growth. This programming happens while the eggs are still maturing in the mother's ovaries. A peptide neurohormone called diapause hormone (DH), released by cells in the mother's subesophageal ganglion, triggers this process. These diapausing eggs are typically laid in the autumn. Once the eggs enter this developmental pause, they require at least two months of cold exposure, at around 5˚C or lower, to exit their arrested state. This cold period breaks the diapause, allowing development to resume after the exposure. In nature, this mechanism ensures that fertilized eggs laid in autumn do not mistakenly hatch before winter. Instead, the fertilized eggs remain dormant through the cold months and only hatch once winter has ended [15-17].

The migratory locust *Locusta migratoria* offers a fascinating example of how embryonic diapause is used to adapt to seasonal changes. These locusts show clear patterns in their reproduction based on latitude. At high, cold latitudes, they produce only one generation per year, while at mid-latitudes, they can produce two generations, and in warmer regions, they may complete three or four generations annually. Each female lays multiple batches of eggs during her lifetime. If the mother experiences long daylight hours, her eggs develop immediately into new locusts. However, when the mother is exposed to short days, the eggs enter embryonic diapause. In autumn, as days grow shorter, all mothers in the population produce diapausing eggs, halting reproduction entirely for the season. Winter's cold is necessary to end this diapause, allowing the eggs to resume development in the next spring. These diapausing eggs - which have overwintered - hatch into the season's first adults, restarting the reproductive cycle. This process ensures that the population's reproductive cycle restarts each spring, as it is physiologically programmed to pause during the winter months [8-10, 13-15].

Larval Diapause

Larval or nymphal diapause is a common phenomenon observed in various insect groups, including Lepidoptera, Diptera, Hymenoptera, Coleoptera, Neuroptera, Odonata, Orthoptera, Hemiptera, and Plecoptera [8-10]. In Lepidoptera, diapause most often occurs at the end of the final larval stage, when the larvae have reached their full size and stopped feeding. However, in certain insects like the mosquito *Anopheles barberi*, diapause usually takes place during the second larval instar, though some individuals may also enter diapause in the third instar. One of the most extensively studied cases of larval diapause in this group is found in *Nasonia vitripennis*, an ectoparasitoid wasp [8-10, 13-15].

Pupal Diapause

Pupal diapause is most commonly observed in Lepidoptera and Diptera, though it is also found in some Hymenoptera. Some of the most notable examples include the saturniid moth *Hyalophora cecropia*, the tobacco hornworm *Manduca sexta*, the flesh fly *Sarcophaga argyrostoma*, and the fruit flies of the genus *Rhagoletis*. However, pupal diapause is entirely absent in Coleoptera, the largest order of insects [13-16]. This developmental arrest usually occurs in the true pupal stage, before the adult form begins to differentiate. In some moth species, however, diapause occurs in the pharate adult stage—when the insect has fully developed into an adult but remains enclosed within the pupal cuticle [13-18].

Adult Diapause

Adult diapause is marked by a halt in the development of reproductive organs, including the ovaries, testes, accessory glands, and other related structures. During this phase, feeding, movement, and mating behaviors are suppressed, and in some cases, the flight muscles may degenerate. This form of diapause is widespread across multiple insect groups, including Coleoptera, Lepidoptera, Diptera, Hemiptera, Orthoptera, Neuroptera, Trichoptera, and Thysanoptera [8, 10-11, 16].

Typically, adult diapause occurs in newly emerged adults that have not yet become reproductively active. These individuals remain in a state of reproductive dormancy until diapause ends. However, there are exceptions where insects enter diapause after a brief period of reproduction. For instance, the leaf beetle *Diorhabda elongata* can switch to diapause after laying eggs when exposed to shorter day lengths. Similarly, female Colorado potato beetles (*Leptinotarsa decemlineata*) may lay a small number of eggs before entering summer diapause [8, 10, 17-18].

Some species can cycle in and out of adult diapause multiple times. In certain cases, newly emerged adults require a short period of feeding before they can enter diapause. For example, if the two-spotted spider mite (*Tetranychus urticae*) does not feed, it fails to develop the characteristic bright orange diapause coloration, and fewer individuals successfully enter diapause. During adult diapause, mating behavior is largely suppressed in both males and females. Accessory glands do not develop, spermatogenesis comes to a halt, and most undifferentiated sperm cells degenerate [8-10, 13]. In certain species, only adult females undergo diapause, while males do not. For example, in the northern house mosquito (*Culex pipiens*), males mate with females in the autumn and then die before winter. The inseminated females enter diapause and survive through the cold months, ensuring the continuation of the species when conditions become favorable again [7-8].

Phases of Diapause

Diapause, a complex physiological state in insects, is divided into several phases

1. Pre-Diapause: Pre-diapause refers to the period when an insect goes through environmental programming (called diapause induction) and also undergoes preparatory physiological changes before entering diapause. These two aspects of pre-diapause — induction and preparation — are usually separate in time, though in some species they may overlap. The pre-diapause phase often starts long before the environment becomes unfavorable for growth or survival. Importantly, entering diapause is not a sudden or immediate response; it happens gradually, with slow and steady internal changes [7-10, 13-15].

The main environmental signals (called token cues) that trigger diapause are changes in day length and temperature. However, other factors can also influence whether an insect chooses to enter diapause. These include poor nutrition, lack of water, aging or declining quality of food resources, overcrowding, drought, dehydration, the mother's diet, the mother’s age when laying eggs, and the environmental conditions the mother experienced during her development or egg formation (oogenesis) [7-11, 19].

In some parasitic insects (parasitoids), diapause is linked to the life cycle of their host: the parasitoid enters diapause when its host does. In such cases, the parasitoid’s diapause timing is controlled by the host’s hormonal system. Interestingly, sometimes a parasitoid living inside a host can even prevent the host from entering diapause, even if the host normally would have [7-11, 13-15].

2. Diapause: Diapause refers to the entire period when during which insect development is halted or greatly slowed, even when external environmental conditions are favorable [7-11]. It consists of three distinct phases:

- **Diapause Initiation (Onset):** During the initiation phase, the insect’s development either stops completely or slows down significantly. At this time, the metabolic rate usually drops, although in some cases the insect may still continue feeding and storing energy. As diapause progresses during initiation, it becomes harder and harder for external factors to reverse the insect’s decision to enter diapause. Initiation is often marked by a clear event, like the insect molting into a specific diapause stage, sometimes with distinctive colors or body features [7-10]. However, in some cases, confirming that diapause has started requires dissecting the insect to check for internal changes — for example, ovaries may stop growing, and eggs may fail to develop during diapause. A reduction in metabolic activity, often measured by a drop in oxygen consumption, is another sign of diapause initiation. However, in species that stay active during diapause, this decrease in metabolism can happen slowly over time [7-10]. Once diapause has been initiated, the insect usually stays in that state for weeks or even months, regardless of whether the environment becomes favorable for development during that period [13-15].

- **Diapause Maintenance:** The maintenance phase of diapause is the longest phase, lasting from when diapause starts to when it ends. During this time, the insect gradually gains the ability to end diapause [13-16].

- **Diapause Termination:** Diapause termination is the point when diapause is truly over, and the insect is physiologically ready to resume its paused development — if the environmental conditions are right. This moment marks a quick shift in development, signaling the end of diapause. However, even though diapause termination happens, the insect may not immediately begin developing. Ending diapause is usually a slow and gradual process. It often relies on certain environmental signals, known as token stimuli. For example, in adult *Listronotus maculicollis* beetles

(Coleoptera: Curculionidae), exposure to a certain amount of winter cold was necessary to experimentally end diapause. In general, environmental factors play a key role in signaling when diapause should end. Prior to the termination of diapause development is arrested and cannot be resumed even under favorable conditions [8-10, 13, 16].

3. Post-Diapause: Post-diapause refers to all the developmental changes that happen after diapause has ended. One important part of this phase is post-diapause quiescence, which is the time between the end of diapause and the actual restart of the halted development. In temperate regions, this period can last for several months. For example, in colder northern areas, diapause might end in early winter, but development will not resume again until the weather warms up in spring. This is because the cold temperatures of late winter are not suitable for development [8-10, 13, 16].

It is often hard to tell the difference between diapause and post-diapause quiescence just by looking at the insect, because they appear the same. The main difference is that after diapause has ended, the insect is *capable* of restarting its halted development if the environment becomes favorable. Even though they look alike, this distinction is very important when studying insect development and predicting when they will become active in spring [8-10, 13, 16].

Once the post-diapause quiescent period ends and environmental conditions improve, the insect restarts its development. The development that follows usually proceeds in a similar way to insects that never entered diapause, ensuring synchronization with seasonal changes. However, insects that have gone through diapause sometimes show reduced fitness—such as slower growth or lower reproductive success—compared to those that did not undergo diapause [13, 16-17].

Winter Diapause Versus Summer Diapause

Most insects that enter a winter diapause usually do so when the days begin to shorten in late summer or early autumn. This response to day length is often reinforced by lower temperatures [13-15, 18].

However, diapause is not solely about surviving the cold of winter. Some insects also enter a summer diapause, even when environmental conditions are favorable for growth. This suggests that diapause also helps insects stay synchronized with the availability of food [7-10, 13-16].

Avoiding parasitoids may also drive summer diapause. For example, the white butterfly *Pieris brassicae* may use this strategy to reduce its risk from natural enemies. Scientists once believed that summer diapause occurred only in hot and dry (arid or Mediterranean) regions. However, later studies have shown that it occurs across a wide range of climates — from places like Finland, Alaska, and Canada to warmer regions — and it has been observed in nearly all major insect groups, including mites [8-10, 18].

Summer diapause typically occurs during the hottest part of the year and is distinct from tropical diapause, which is common in insects from tropical regions and helps them time their activity with wet and dry seasons. Insects that enter diapause in mid- or late summer and remain dormant through winter are not considered to be in summer diapause. True summer diapause ends in autumn as temperatures drop and days grow shorter [8-10, 18].

A common pattern among many insects is to be active in spring, feeding on new plant growth or other insects, then become dormant during summer. As days shorten and temperatures fall in autumn, they may become active again. Reproduction may occur either before or after summer diapause—or even both. Afterwards, the insect may enter winter diapause at a different life stage or remain active if conditions permit [13-16].

One example is the bug *Poecilocoris lewisi*, which enters winter diapause as a fifth-instar nymph in response to short days. Then, in spring, it responds to long days by entering summer diapause as an adult. This pause in activity helps synchronize its life cycle with the release of seeds from its host plant, *Cornus controversa*, in July [7-10, 13-16].

Insects often enter summer diapause in response to long daylight hours and high temperatures. For instance, in the burying beetle *Nicrophorus quadripunctatus*, these environmental cues trigger summer diapause. While the seasonal depletion of food is often the primary evolutionary reason for summer diapause, competition for the remaining food may also contribute [8, 13-16].

During both summer and winter diapause, insects typically accumulate energy reserves such as fats and glycogen. Metabolic activity also drops significantly in both types of diapause. In the onion maggot *Delia antiqua*, molecular markers of diapause — such as increased activity of genes encoding heat shock proteins — are present in both summer and winter diapause. However, different gene sets are more active in each: winter diapause shows higher expression of genes linked to fat metabolism, while summer diapause exhibits stronger activation of immune-related genes [8, 10, 15-16].

Diversity and Trade-Offs in Insect Diapause

Rich diversity of diapause traits exists within insect populations. Natural variation in insect diapause affects not only when diapause begins but also how long it lasts. For example, in the subtropical cockroach *Symploce japonica*, most individuals end diapause within a short period, but some remain in diapause for much longer [8-10, 15-16].

This variability allows natural selection to shape diapause responses that are better adapted to changing environments. Such diversity functions as a *"bet-hedging" strategy:* if not all individuals respond identically, some may survive and thrive under unexpected environmental conditions, thereby increasing the species' overall chance of survival. Variation in diapause traits can also enable rare forms to colonize new areas or adjust to changes in seasonal food availability [13, 15-18].

In some species, individuals can enter and exit diapause more than once during the same life stage. For instance, adult males of the grasshopper *Oedipoda miniata* in Israel can repeatedly enter and emerge from diapause in response to changing daylengths [8-10, 15-16].

One clear consequence of diapause is a reduction in the number of generations that can occur within a year, as part of the annual cycle is spent in a non-reproductive, dormant state [8-11].

Although diapause is often thought to help insects survive unfavorable conditions, it does not always guarantee survival. For example, the larvae of the hemlock woolly adelgid (*Adelges tsugae*) suffer high mortality during summer dormancy [13-15].

Other potential downsides of diapause include depletion of energy reserves, smaller body size, reduced egg production, delayed egg-laying, shorter adult lifespan after diapause, and a lower number of generations per year [8-10, 14-16].

The Role of Photoperiodism in Insect Diapause

Photoperiod is the length of time an organism is exposed to light during a 24-hour period — in other words, the duration of daylight in a day. It varies with the seasons: days are longer in summer and shorter in winter. A type of timing system — called the photoperiodic clock — helps insects track seasonal changes in day length to control diapause [4-5, 12, 19]. The photoreceptor, typically located in the brain or eyes, detects changes in light duration. The circadian clock acts as a timekeeping system that helps measure the length of day or night within a single 24-hour cycle, while the photoperiodic clocks determine whether the light-dark cycle qualifies as long or short. Finally, a counter mechanism records the number of successive long or short days, and once a threshold is reached, it triggers endocrine changes that initiate or terminate diapause [4-5, 12, 19].

Photoperiodism depends on two components: a timer that measures the duration of each day or night, and a counter that keeps track of how many successive short or long days have passed before triggering a response such as diapause. The day length at which 50 percent of an insect population enters diapause is called the critical day length; it is a genetically determined trait [12, 19].

Nutritional and Ecological Cues Regulating Diapause in Insects

To enter diapause, insect larvae usually need to reach a certain body weight—around 600 mg in some beetle species. If they weigh less than this threshold, they typically do not enter diapause. Interestingly, beetles that experience starvation tend to remain in diapause for a longer duration. A similar effect is observed in the swallowtail butterfly *Atrophaneura alcinous*: larvae deprived of food every other day during the first 10 days of life exhibit a longer pupal diapause compared to those that are regularly fed. However, this starvation-induced extension of diapause is not universal. For example, in the fly *Chymomyza costata*, starvation has no noticeable effect on larval diapause [10, 11, 13, 15, 16].

As the season progresses, the nutritional quality of host plants often declines. This decline can serve as a seasonal cue, promoting diapause in many insect species. In the cabbage beetle *Colaphellus bowringi*, larvae that feed on young radish leaves show a low incidence of diapause, whereas those feed on mature leaves are more likely to enter diapause. In the swallowtail butterfly *Byasa alcinous*, even larvae from the same mother can differ in diapause response. Those feeding on tougher, older leaves of their host plant (*Aristolochia kaempferi*) are more likely to enter pupal diapause than those feeding on younger leaves (8-10).

A similar trend is observed in monarch butterflies (*Danaus plexippus*): adults raised on older milkweed plants are more likely to enter diapause than those raised on younger plants. Interestingly, monarch larvae raised on tropical milkweed, a non-native plant in North America, often skip diapause and migration, resulting in the formation of resident populations [13-16].

In the maize stemborer *Chilo*, feeding on older maize stems—low in protein—promotes larval diapause. For predatory insects and parasitoids, seasonal changes in prey or host availability and quality of food can also act as cues to trigger diapause. In parasitoids, the effects of food scarcity often manifest in their offspring rather than in the female herself. For instance, in *Nasonia vitripennis*, females denied access to a host shortly after emerging tend to produce more offspring that enter diapause [8-11].

Parasitoids of insects that produce only one generation per year (univoltine hosts) tend to undergo obligatory diapause. Conversely, parasitoids of insects with multiple generations per year (polyvoltine hosts) rely on environmental cues such as temperature, photoperiod, host availability, and even the condition of the host plant to determine whether to enter diapause [8-11] .

Maternal Regulation of Diapause

The duration and likelihood (incidence) of diapause in offspring can be strongly influenced by the environmental conditions experienced by the mother, particularly photoperiod (day length) and temperature. In the blow fly *Lucilia sericata*, when the parental generation is exposed to short days and high temperatures (25˚C vs. 17.5˚C), their offspring undergo a longer larval diapause [8-11, 14, 17].

Eggs destined for diapause often differ physically from non-diapause eggs. They are generally larger and contain more lipid reserves. For instance, diapausing eggs of the mosquito *Aedes albopictus* contain more lipids. However, this increased size is likely a consequence of the diapause program rather than its cause. In the yellow dung fly *Scathophaga stercoraria*, eggs with higher lipid content are more likely to develop into pupae that enter diapause [8-11, 14].

In the flesh fly *Sarcophaga bullata*, the photoperiod history of the mother plays a crucial role in determining whether her offspring enter diapause. For example, if a pupa is exposed to long-day conditions during its embryonic and larval stages, it does not enter diapause. In contrast, a pupa from a mother reared under long-day conditions retains the ability to respond to short-day cues by entering diapause. However, a pupa from a mother reared under short-day conditions fails to respond to short-day signals and, consequently, does not enter diapause. This maternal influence of photoperiod on the developmental trajectory of the offspring is a classic example of a maternal effect [17, 22].

Physiological Preparations for Diapause

To survive the long, dormant period of diapause, insects often store extra energy in advance. This energy is usually stored in the form of triacylglycerides (TAGs), but glycogen and hexamerins also increase. For instance, in the Asian tiger mosquito (*Aedes albopictus*), mothers allocate about 30% more lipids to eggs destined for diapause. Diapausing larvae of the burnet moth (*Zygaena trifolii*) contain twice as much fat as non-diapausing ones. Similarly, in the parasitoid *Praon volucre*, diapausing larvae are nearly 30% heavier in weight compared to non-diapausing individuals, primarily owing to lipid accumulation [8-10, 23-25].

Hexamerin storage proteins also increase significantly in diapausing individuals of various species, such as the southwestern corn borer (*Diatraea grandiosella*), the Colorado potato beetle (*Leptinotarsa decemlineata*), and the linden bug (*Pyrrhocoris apterus*) [8-10, 13-16].

Phenotypic Changes Associated with Insect Diapause

Insects preparing for diapause often develop different colors or patterns on their bodies compared to their active, non-diapause forms. These color changes sometimes help them blend more effectively with their surroundings during dry or cold seasons, making them less visible to predators [8-11].

Such differences in coloration can be observed at various developmental stages — even in embryos. For example, the non-diapause eggs of the silkworm (*Bombyx mori*) are pale yellow-white, whereas the diapause eggs are much darker. This difference arises because diapause eggs contain high concentrations of pigments called ommochromes and their precursor, 3-hydroxykynurenine. These pigments are found in both the eggshell (chorion) and the membrane beneath it (serosa) and are absent in non-diapause eggs. Color changes also occur in adult moths. In the Diazo race of *Bombyx mori*, adults that produce diapause eggs in autumn display dark brown bands on their forewings, while summer adults, which do not enter diapause, lack these markings [8-13].

Color variation, known as color polyphenism, is particularly striking in some tropical butterflies and moths. For instance, the West African butterfly *Precis octavia* is bright orange with black markings during the wet season, but during the dry season — when it enters reproductive diapause — it appears mostly dark, with blue spots and very little orange. In the Eurasian nymphalid butterfly *Araschnia levana*, individuals that develop into adults during the summer—without undergoing diapause—exhibit a black-and-white wing pattern (Figure 1). In contrast, those that emerge in the spring after spending the winter in pupal diapause are mostly orange in color. In many insects, seasonal coloration helps them match their environment. For example, the green lacewing (*Chrysoperla carnea*) is green in summer, blending with leaves, but turns brown in autumn during diapause to match dried foliage [8-11, 13-16].

Fig 1: The Eurasian nymphalid butterfly *Araschnia levana* shows a remarkable example of seasonal polyphenism. Individuals that emerge in the spring—after overwintering in the pupal stage—are primarily orange in coloration. In contrast, adults that develop in the summer, without undergoing diapause, have wings with a distinctive black-and-white pattern. [Image source: www.ukbutterflies.co.uk]

In addition to color changes, insects may also show morphological differences depending on whether they are destined for diapause. In the water strider *Gerris lacustris*, the first summer generation develops short wings (brachypterous), small flight muscles, and begins reproduction early. In contrast, adults from the late summer generation have long wings (macropterous), larger flight muscles, and delay reproduction — a trade-off that enables them to fly to safe overwintering sites [8-12, 26].

In another species, the linden bug (*Pyrrhocoris apterus*), short-day conditions induce reproductive diapause and lead to the development of short wings. When raised under long-day conditions at the same temperature, the bugs bypass diapause, start reproducing immediately, and grow long wings. Interestingly, both morphs are flightless — suggesting that the difference in wing size may not serve a functional purpose in flight, but instead reflects an internal season-specific program [26].

Site Selection and Behavioral Strategies in Diapausing Insects

To survive the long and harsh period of diapause, insects must carefully select safe hiding spots that offer protection from extreme weather, predators, parasites, and diseases. For example, when given a choice, the adult apple blossom weevil (*Anthonomus pomorum*) prefers to overwinter in dry leaf litter rather than on smooth bark, grass, or soil. Their survival rate is also higher in these preferred locations. Similarly, while the summer generation of the leaf beetle (*Chrysomela lapponica*) feeds and develops on willow leaves, individuals preparing for winter diapause burrow into the soil to take shelter. Diapausing adult female mosquitoes (*Culex pipiens*) seek cool, dark, and moist environments—such as basements or caves—that help prevent dehydration [8-11, 13-15].

Underground overwintering is common among many insects undergoing diapause. For instance, the northern house mosquito (*Culex pipiens*) seeks refuge in caves, basements, culverts, and cisterns. Predatory mites like *Euseius finlandicus* hide under loose bark, inside empty insect scales, or within deep cracks and old wounds on peach trees. Some insects even lay their eggs inside the dead bodies of adult females — as seen in the red-legged earth mite (*Halotydeus destructor*) — to shield them during diapause [7-10].

Once an insect finds a suitable hiding place, it often reinforces it. Many species line their shelters with silk, construct thick cocoons, or apply waterproofing substances. Diapausing cocoons are typically thicker and stronger than those of non-diapausing individuals. These durable cocoons help absorb solar heat, block ultraviolet radiation, prevent cuticle damage, deter fungi and bacteria, and offer protection from predators [7-10].

Preventing water loss is also critical during the dry winter months. In some insect species, such as the soybean pod borer (*Leguminivora glycinivorella*), diapausing cocoons help prevent both desiccation and waterlogging. Other insects waterproof their shelters with wax, resin, or oily substances — like the neotropical bee (*Epicharis zonata*) or the puparia of flesh flies. Even the outer shell (chorion) of diapausing mite embryos can become thicker and darker, offering better protection against heat and dryness. The brine shrimp (*Artemia franciscana*) encloses its diapause embryos within a tough chitinous shell called a cyst, which is highly resistant to environmental stress [8-10, 13-16].

A few insect species that undergo diapause also undertake long-distance migrations as part of their seasonal survival strategy. One of the most well-known examples is the monarch butterfly (*Danaus plexippus*). Each year, monarchs born in late summer enter a state of adult diapause, characterized by arrested reproductive development, increased fat storage, and an extended lifespan. This generation, often referred to as the “migratory generation,” undertakes a southward journey (Figure 2) spanning up to 4,000 kilometers, heading to overwintering sites in central Mexico (eastern populations) or coastal California (western populations), allowing them to survive seasonal changes in temperate North America. The induction of adult diapause in the “migratory generation” of monarchs is triggered by shortening day length and cooler temperatures, which suppress JH levels and delay gonadal development. This physiological state enables monarchs to survive the winter without reproducing. The migratory generation flies south in the fall and overwinters. In contrast, the successive spring and summer generations are born along the northward route, reproduce en route, and gradually repopulate the northern breeding grounds. In spring, rising temperatures and increasing day length terminate diapause. The butterflies resume reproductive activity during their northward migration, laying eggs only where milkweed—their sole larval food source—is available. Importantly, no single monarch completes the entire round-trip journey. The annual migration cycle is a multi-generational process, typically requiring 3 to 5 generations to complete [27].

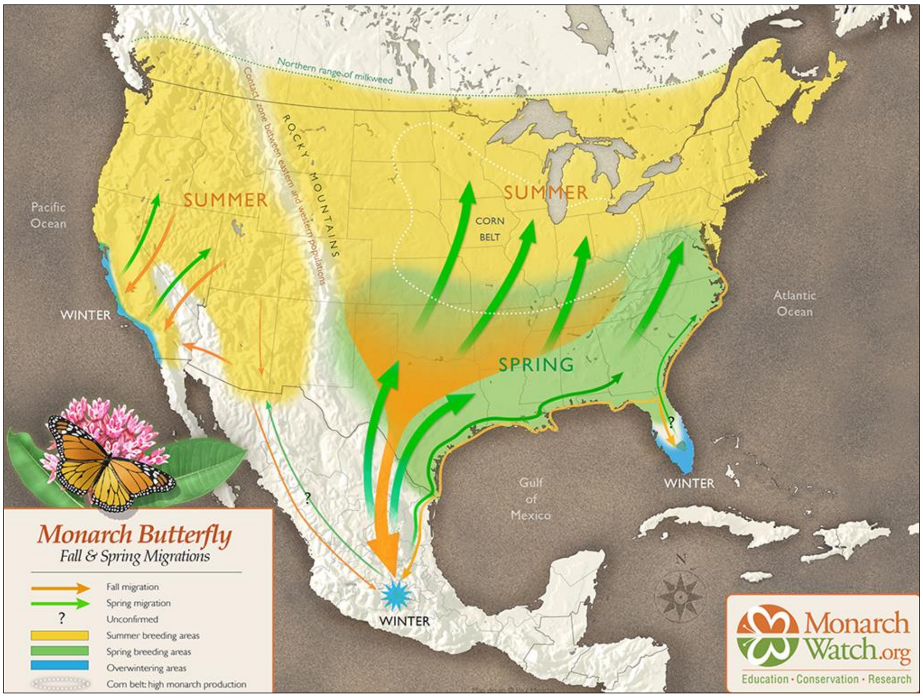

Fig 2: The autumn migration patterns of monarch butterflies (*Danaus plexippus*), shown in orange, indicate movement from the northern United States and Canada toward central Mexico and the southern coast of California. In contrast, the spring return migration, shown in green, traces their gradual recolonization of northern habitats. [Image source: www.monarchwatch.org]

Many diapausing insects aggregate in large groups at overwintering or aestivation sites. The monarch butterflies congregate by the millions in Mexican forests to overwinter. At some sites, over 14 million monarchs have been found clustered on just a few acres of trees. Similarly, up to 40 million lady beetles (*Hippodamia convergens*) have been observed gathering near the snowline in California’s mountains [8-10, 27-28].

There are clear advantages to such aggregations. In addition to protection from predators, forming large groups creates a shared microenvironment that reduces water loss and blocks harmful radiation. For example, in the beetle *Stenotarsus rotundus*, groupings can be up to eight layers deep, which helps reduce metabolic rates. As group size increases, oxygen consumption drops, which in turn conserves water. In the shield bug (*Parastrachia japonensis*), individuals in groups use only half as much oxygen as solitary ones. This communal living during diapause helps insects conserve both energy and water [7-10, 14-15].

Unusual Molting Behavior During Insect Diapause

Some insects even molt during diapause, which is unusual because diapause is typically a time when growth and development pause. This kind of molting is common in certain moth larvae (such as pyralids and noctuids) and in crickets. Examples include the southwestern corn borer (*Diatraea grandiosella*), the Mediterranean corn borer (*Sesamia nonagrioides*), the rice stem borer (*Chilo suppressalis*), the African maize stalk borer (*Busseola fusca*), and the cricket *Modicogryllus siamensis* [7-10].

In some species, such as *S. nonagrioides*, insects can molt five to six extra times during diapause. These molts are called *stationary molts* because they do not result in any significant increase in body size or weight of the larvae. This condition is linked to persistently high levels of juvenile hormone (JH) [7-10].

Environmental Influences on Diapause Duration and Termination in Insects

The duration of diapause, or how long an insect stays in this dormant state under certain environmental conditions, is influenced by various environmental factors, many of which vary by species. For some insect species, chilling (cold temperatures) is necessary to end diapause, while for others, it is not. The daylength (photoperiod) is important for initiating diapause, but it plays a smaller role in determining how long diapause lasts for most species [10, 13, 16].

In insects from temperate regions, diapause often begins in the autumn and lasts until the winter solstice. At this point, diapause ends, and a period of post-diapause quiescence starts. During post-diapause quiescence, the insect is fully capable of development but remains inactive because temperatures are too low for development to proceed. Development only resumes once temperatures rise in the spring [8, 10, 13, 16].

In the giant silk moth *Hyalophora cecropia*, which is univoltine (producing one generation per year), diapause begins soon after pupation. In experiments with *Hyalophora cecropia*, researchers found that a 10-week chilling period at 5˚C was needed to break diapause in pupae. Interestingly, only the brain needs to be chilled, not the entire body. Similarly, the silk moth *Bombyx mori* requires two months of chilling at 5˚C to break its embryonic diapause. On the other hand, the solitary bee (*Osmia lignaria*) requires only a brief chilling period, as short as one week at 4˚C to end diapause [8, 10, 13, 16].

However, not all insects require chilling to break diapause. For instance, the Colorado potato beetle (*Leptinotarsa decemlineata*) can exit diapause at temperatures ranging from 4˚C to 25˚C, with higher temperatures accelerating the process [8, 10, 23].

In species like the fruit moth (*Adoxophyes orana*), a period of low temperature is not required for larval diapause. However, photoperiod (day length) influences diapause; short days maintain the diapause state, while long days signal its termination. Similarly, in the linden bug (*Pyrrhocoris apterus*), photoperiodic cues are used to end diapause, but these cues are only effective at temperatures above 15˚C, and the bug requires food to resume development [8, 10, 26].

Hormonal Regulation of Diapause in Insects

Diapause during the larval and pupal stages—and possibly even in late-stage embryos—occurs mainly owing to the absence of the steroid hormone ecdysone, which is essential for growth and molting in insects. Normally, the release of ecdysteroids (such as ecdysone) from the prothoracic glands is triggered by another hormone called prothoracicotropic hormone (PTTH). If PTTH, a brain neuropeptide hormone, is not released, the insect cannot continue developing [1-3, 28].

Juvenile hormone (JH), an acyclic sesquiterpene produced by the corpora allata, prevent metamorphosis when present in high levels in an insect larva. Instead of transforming into a pupa or adult, the insect molts into another larval stage when the levels of JH are high. In adult females, JH stimulates vitellogenesis—the production of vitellogenin (an egg yolk protein) in the fat body—and also promotes ovarian development, facilitating egg maturation [1-3, 28].

In the larvae of many insects, high levels of JH can inhibit the release of PTTH, thereby preventing ecdysone production and halting development. However, this is not always the case. In some insects, JH plays a role only at the beginning of diapause, while in others—such as the wasp *Nasonia*—JH does not appear to be involved at all. In the pupal stage of moths and butterflies, the suppression of PTTH release also does not seem to be caused by elevated JH levels [1-3, 28].

In insects that undergo diapause during the larval or pupal stages, the hormone ecdysone typically plays a crucial role. Diapause can occur either because the brain fails to release PTTH (prothoracicotropic hormone) or because the prothoracic gland does not respond to PTTH—at least not until it has been exposed to cold temperatures for a certain period. Without PTTH, the prothoracic gland does not produce ecdysone, and development is arrested resulting in diapause [8, 10, 28].

In adult insects, diapause is primarily caused by the absence of juvenile hormone (JH). In several species, adult insects enter reproductive diapause before the onset of winter. This form of diapause is typically triggered by the absence of JH. Absence of JH leads to inhibition of vitellogenesis (yolk formation) in adult females resulting in ovarian arrest. JH often rises again toward the end of diapause when environmental cues become favorable. This rise of JH resumes development or reproduction depending on the life stage. Topical application of JH analogs (like methoprene) can break diapause artificially in many insects [8, 10, 28].

Embryonic diapause that occurs early in development is controlled by a diapause hormone (DH) produced by the mother insects. In the silkworm *Bombyx mori*, this hormone has been identified as a 24-amino acid-long peptide derived from a larger protein precursor, which also gives rise to another important hormone called PBAN (pheromone biosynthesis-activating neuropeptide). Laboratory experiments using embryos grown from dechorionated eggs (eggs with their outer layers removed) show that the diapause hormone (DH) acts on the mother's ovaries, not directly on the eggs or embryos. DH also induces pigment changes in a membrane called the serosa, owing to the uptake of 3-hydroxykynurenine, which is then converted into a pigment known as ommochrome [17, 22, 28].

Diapause hormone (DH) is produced by adult females of *Bombyx mori* that have experienced the long daylight hours of midsummer. This hormone helps prepare the next generation for harsh conditions by inducing diapause in their developing eggs. Diapause prevents the eggs from hatching and developing during autumn and winter, when environmental conditions are unfavorable. In this way, the embryo depends on maternal cues to determine whether it should enter diapause [17, 22, 28].

When larvae of *Bombyx mori* are exposed to short photoperiods, the adults they develop into later produce DH from neurosecretory cells located in the subesophageal ganglion. This hormone is transferred into the eggs and causes the developing embryos to pause at the gastrulation stage [17, 28].

DH functions by stimulating the production of the enzyme trehalase in the ovaries. Trehalase converts trehalose—a sugar found in the insect's hemolymph—into glycogen, which accumulates in the yolk of the developing oocytes. Later, some of this glycogen is converted into sorbitol and glycerol, which help maintain diapause. These two compounds act as cryoprotectants, enabling the embryo to survive freezing temperatures. Additionally, sorbitol directly inhibits further embryonic development. In this way, DH regulates glycogen storage and utilization within the diapause eggs. However, in non-diapause eggs, glycogen levels remain high [17, 22, 28].

To terminate embryonic diapause in *Bombyx mori*, the eggs must be exposed to prolonged cold (chilling). This cold exposure leads to the conversion of sorbitol and glycerol back into glycogen, which removes the developmental block and supplies the energy needed for the embryo to resume development and hatch. This DH-based diapause mechanism has, so far, been observed only in the silkworm *Bombyx mori*, a lepidopteran insect [17, 22, 28].

Bombyx mori eggs that enter diapause also contain maternal ecdysteroids in an inactive, phosphorylated form. In eggs that do not enter diapause, these ecdysteroids are converted into their active forms, particularly 20-hydroxyecdysone (20E). Eggs that proceed with normal development show a rise in free 20E levels, which is associated with embryonic molting and progression of development. In contrast, diapause eggs maintain low levels of free 20E throughout the arrested period [17, 22, 28].

Concluding Remarks

Diapause, a temporary, predetermined cessation of growth and development in insects, plays a vital role in their life cycles, reproductive strategies, and evolutionary success. It is a highly adaptive and evolutionarily conserved form of developmental arrest in insects that enables survival under unfavorable environmental conditions. This complex, multistep phenomenon is regulated by intricate interactions between environmental cues—primarily photoperiod and temperature—and endogenous hormonal and molecular pathways.

Recent advances in genomics, transcriptomics, and gene-editing technologies such as CRISPR-Cas9 have opened new avenues for dissecting the molecular mechanisms underlying insect diapause. These tools are revealing both species-specific variations and conserved regulatory modules, offering deeper insights into how diapause, a genetically programmed survival strategy, is modulated across diverse ecological contexts.

Understanding insect diapause holds significant implications for pest management, pollinator conservation, and predicting insect responses to climate change. Future research that integrates ecological, physiological, and molecular approaches will be essential to fully unravel the complexity of diapause in insects. Such interdisciplinary efforts will not only enhance our knowledge of insect biology but also aid in developing strategies to mitigate the harmful impact of insects on both agricultural and natural ecosystems.

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