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Diverse adaptations in insects: A Review

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Abstract

Changing environment demands organisms to change in order to survive. Organisms respond to their environments by making different types of adaptations. Adaptations are essentially a product of natural selection. As populations are subjected to vagaries of climate, the genetic characteristics that are well suited to the environment are selected. Insects are found in a wide range of environment experiencing extremes of biotic as well as abiotic factors. To survive the environmental extremes, to escape or alleviate adversities of environment, insects have evolved a number of physiological, behavioural and morphological adaptations. Behavioural responses include burrowing into substrate and being active only through a restricted period of the day. Furthermore, insects may feign death, a response termed thanatosis. It is obvious that at least some of the colours and patterns (Crypsis and Mimicry) serve a defensive function by offering a degree of protection from predators and to adapt in the environment. As a group, insects have limited ability to regulate their body temperature and have thus required a range of strategies to support life in thermally stressful environments (low as well as high temperature), including behavioural avoidance through migration and seasonal changes in cold tolerance. With respect to cold stress, insects have traditionally been divided into two main groups: freeze tolerant and freeze avoiding, although this simple classification is underpinned by a complex of interacting processes, i.e. synthesis of ice nucleating agents, cryoprotectants, antifreeze proteins and changes in membrane lipid composition and the change in membrane permeability, reduction in transpiration rate and synthesis of heat shock proteins help the insects to thrive under high temperature conditions. Thus it may be said that adaptations (physiological, behavioural and morphological adaptations) have played a leading role in insects to become the most dominant organisms on the earth's surface.

Keywords: Adaptations, environment, insects, mechanisms

Introduction

Organisms experience wide range of environmental extremes. The environment does not produce the variation but selects them. A particular environment acts as a screen, permitting certain individuals to continue inhabit it and eliminate others. In response to environmental conditions organisms evolve a range of adaptive strategies. An organism having a genotype which gives it some selective advantage in a particular environment is said to be adapted to that environment and the characteristics which are useful in that environment are called adaptations**.** Insects are found in a wide range of environment experiencing extremes of biotic as well as abiotic factors [1]

Adaptation is essentially a product of natural selection acting on the populations. Natural selection means differential reproduction i.e. some members of population have traits which enable them to grow up and reproduce at a high rate and leave the more offsprings in the next generations than others [2]**.** Generally those individuals which are best adapted to the environment have a greater number of surviving young ones. The well adapted individuals on the whole are healthier, can find food and mate readily.

Adaptations may refer to an organism's ability to change in order to cope with changing environmental circumstances. Also it may be a special feature or behaviour that makes an organism particularly suited to its habitat. The following categories of adaptations are recognised: (1) Behavioral (2) Morphological (3) Physiological. Behavioural adaptations deal with an organism's actions, either solitarily or as a group. Behavior is what animals do. It can be defined more precisely as an internally directed system of adaptive activities that facilitate survival and reproduction. Innate behavior is genetically programmed. Individuals inherit a suite of behaviors (often called an ethogram) just as they inherit physical traits such as body color and wing venation. In general, innate behaviors are:

1. Heritable -- encoded in DNA and passed from generation to generation
2. Intrinsic -- present in animals raised in isolation from others

3. Stereotypic -- performed in the same way each time by each individual
4. Inflexible -- not modified by development or experience
5. Consummate -- fully developed or expressed at first performance

Since innate behavior is encoded in DNA, it is subject to genetic change through mutation, recombination and natural selection. One species of dance fly (Fig. 1) has a courtship ritual in which a male gives a ball of silk to a female. She unravels the ball while he mates with her. By itself, this curious behavior seems truly bizarre. But a study of courtship in other dance flies reveal that males use a nuptial gift as a way to divert a female's aggressive behavior long enough for insemination to occur

Fig 1: Courtship behaviour shown by dancefly.

Learning can be defined as a persistent change in behavior that occurs as a result of experience. Since a newborn nymph or larva has no prior experience, its first behavior will be entirely innate. Each individual starts life with a "clean slate". It acquires new skills and knowledge through trial and error, observation of other individuals, or memory of past events. In general, learned behaviors are:

1. Non heritable -- acquired only through observation or experience
2. Extrinsic -- absent in animals raised in isolation from others
3. Permutable -- pattern or sequence may change over time
4. Adaptable -- capable of modification to suit changing conditions
5. Progressive -- subject to improvement or refinement through practice

Behavioural Adaptations

Migration

All insects move to some extent. The range of movement can vary from within a few centimetres for some sucking insects and wingless aphids to thousands of kilometres in the case of other insects such as locusts, butterflies and dragonflies. Migratory behaviour is persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends upon some temporary inhibition of station-keeping responses but promotes their eventual disinhibition and recurrence [3]. This disqualifies movements made in the search of resources and which are terminated upon finding of the resource. Migration on the other hand involves longer distance movement and these movements are not affected by the availability of the resource items. All cases of long distance insect migration involves those that are winged [3]. Insect migration is the seasonal movement of insects, particularly those by species of following orders:

Lepidoptera

Migration of butterflies and moths is particularly well known. The Bogong moth is a native insect of Australia that is known to migrate to cooler climates. The Madagascan sunset moth (*Chrysiridia rhipheus*) has migrations of upto thousands of individuals, occurring between the eastern and western ranges of their host plant, when they become depleted or unsuitable for consumption [4]. In southern India, mass migrations of many species occur before monsoons. As many as 250 species of butterflies in India are migratory. These include members of the Pieridae and Nymphalidae [5].The Australian Painted Lady periodically migrates down the cost of Australia, and occasionally, in periods of strong migration in Australia, migrate to New Zealand [6].

Orthoptera

Short-horned grasshoppers sometime form swarms that will make long flights. These are often irregular and may be related to resource availability and thus not fulfilling some definitions of insect migration. There are however some populations of species such as *Schistocerca gregaria* that are thought to make regular seasonal movements in parts of Africa [7].

Odonata

Dragonflies are among the longest distance insect migrants. Many species of *Libellula*, *Sympetrum* and *Pantala* are known for their mass migration [7] (Williams 1957). *Pantala flavescens* is thought to make the longest ocean crossings among insects, flying between India and Africa on their migrations. Their movements are often assisted by winds [8].

Coleoptera

Ladybird beetles such as *Hippodamia convergens*, *Adalia bipunctata* and *Coccinella undecimpunctata* have been noted in large numbers in some places. In some cases, these movements appear to be made in the search for hibernation sites [7].

Hibernation

Insects are known to pass winter through different stages viz. egg, nymph, larvae, pupae, and adults. Only a few, notably the Monarch butterfly, migrate southwards. The Mourning Cloak butterfly spends the winter in barns or sheds or hollow trees. Ladybird beetles hibernate in big colonies under the loose bark of trees, in tree cavities, and in buildings. On warm winter days they may come out and crawl around. House flies, and the blow flies known as Bluebottles and Green bottles, winter in cellars, attics and the crevices of buildings. If the temperature rises above 50 degrees, they will crawl or fly aimlessly about [9]. Many adult insects spend the winter underground. The May beetle or June bug burrows down below the frost line. The young queen bumblebees lie dormant in burrows well below the ground surface. Some beetles, for instance, get ready for hibernation by storing up fat, like bears. Other insects seem to be able to eliminate water from their bodies and can endure freezing temperatures for weeks at a time. In general, uniformly cold winters with plenty of snow are easiest on insect life. Next best are very mild winters with little or no freezing. Cold winters with occasional warm thawing days, and warm winters interrupted by severe cold spells, are both disastrous to many kinds of hibernating insects.

Sounding scary

Many insects, such as some shield bugs (order: Hemiptera; family Pentatomidae), dung beetles (order: Coleoptera; family: Scarabaeidae), longhorn beetles (order: Coleoptera; family: Cerambycidae), ants (order: Hymenoptera; family: Formicidae) and tiger moths (order: Lepidoptera; family: Arctiidae) produce rasping, buzzing or hissing sounds when disturbed or handled, in most cases by rubbing or vibrating one part of the body against another part (a mechanism called stridulation). Death's head hawk moths *Acherontia* sp. (order: Lepidoptera; family: Sphingidae) can make a high pitched squeaking noise when disturbed, by forcing air out of the proboscis (mouthparts); the hissing cockroach (*Gromphadorhina portentosa*) from Madagascar, as its name suggests, can make a hissing sound by expelling air through a modified pair of its abdominal breathing pores (spiracles). These various, apparently defensive, insect sounds may serve to startle or confuse a predatory bird or mammal [10].

Shooting spray

A foul smell or a bad taste is often enough to discourage a potential predator. Shield bugs (often called stink bugs; order: Hemiptera) have specialized glands located in the thorax or abdomen that produce foul-smelling hydrocarbons. These chemicals accumulate in a small reservoir adjacent to the gland and are released onto the body surface only as needed. The larvae of certain swallowtail butterflies (order: Lepidoptera; family: Papilionidae) have eversible glands called osmeteria, located just behind the head. When a caterpillar is disturbed, it rears up everts the osmeteria to release a repellent vapour and waves its body back and forth to ward off intruders. Similar eversible osmeteria, but located on each side of the thorax and abdomen, are found in adult beetles (Coleoptera) belonging to the family Malachidae [11]. The larvae of some leaf beetles (order: Coleoptera: family: Chrysomelidae) cover themselves with their own slimy, black excreta - no doubt distasteful and certainly not an appetizing sight. Irritant compounds often induce cleaning behaviour by a predator giving the prey time to escape. Some blister beetles (order: Coleoptera; family: Meloidae) produce cantharidin, a strong irritant and blistering agent that circulates in their haemolymph. Droplets of this blood ooze from the beetle's leg joints when it is disturbed or threatened - an adaptation known as reflex bleeding. Many ladybirds (order: Coleoptera; family: Coccinellidae) and leaf beetles (order: Coleoptera; family: Chrysomelidae) have similar reflex bleeding mechanisms [12]. Irritant chemical sprays are also produced by some termites (order: Isoptera), cockroaches (order: Dictyoptera), earwigs (order: Dermaptera), stick insects (order: Phasmida) and beetles (order: Coleoptera). In many cases these sprays also contain pungent, repellent substances and their release is sometimes accompanied by a threatening posture or display. Some darkling beetles (order: Coleoptera; family: Tenebrionidae) adopt an aggressive head-stand when disturbed and squirt a pungent, irritating mixture of quinones at their attacker from large glandular reservoirs at the tip of their raised abdomen. Rove beetles (order: Coleoptera; family: Staphylinidae) curl the abdomen upwards and over their back in a scorpion-like manner whilst releasing an irritant spray or vapour from the abdomen tip. The notorious bombardier beetles (order: Coleoptera; family: Carabidae) store chemical precursors for an explosive reaction mixture in very specialized reinforced abdominal glands. When the beetles are threatened, these precursors are mixed together to produce a forceful discharge of boiling hot quinone and water vapour (steam), together with an audible pop [13].

Thanatosis (feigning death)

Death feigning as a defensive response is very widespread in insects. A remarkable example of intraspecific death feigning comes from the fire ants. In the highly territorial species *Solenopsis invicta*, when neighbouring colonies are at war, youngest feign death, after danger has apparently passed, they look around before fully reviving as they are the most vulnerable and ineffective in fight due to their relatively soft cuticle, this seems a sensible strategy, and it was shown that death feigning increases their chances of survival fourfold compared to older workers. This is important, because these young workers have the longest life expectancy and are hence most valuable to the colony [14].

Red flour beetles (*Tribolium castaneum*) feign death upon encountering a predator such as a jumping spider. Artificial selection experiments have shown that the duration of death feigning is variable and heritable. Beetles selected for long-duration thanatosis had a lower frequency of predation when exposed to the jumping spider (*Hasarius adansoni*). A particularly intriguing case of death feigning is found in a pselaphid beetle (*Claviger testaceus*). Entering an ant nest is not an easy proposition, but by feigning death it is treated as a cadaver and the ants (*Lasius flavus*) attempt to dismember it as they drag this beetle to the nest. Once safely ensconced, the beetle unexpectedly revives and not only manages to trick the ants into feeding and caring for it, but also preys on its eggs, larvae and pupae [11]. Death feigning has been reported from several other groups of insects and in different contexts. It serves as an anti-predator adaptation in the nymphs of the blue-tailed damselfly (*Ischnura elegans*) and in the pygmy grasshopper (*Criotettix japonicus*). Emerging queens of the stingless bee (*Melipona beecheii*) feign death to avoid being attacked by their workers and female robber flies (*Efferia varipes*) to evade harassment by males. Males of the praying mantis (*Mantis religiosa*) freeze immediately after mating, apparently so they don't end up as a meal for the female [10].

Web spinning

Web spinning is found in insects belonging to four different orders. The first is one of the small order Embioptera (containing only about 300 species), have got common name web spinners as this is their most noticeable trait. Embids are small, inconspicuous, tropical insects that have silk glands on the tarsi of their front legs. They use this silk to create tunnels where numerous females and their young are protected from desiccation and predators. Another small order possibly closely related is the Psocopterans or booklice, also spin webs. Females of this small and primitive order of insects spin silk in which to hide their eggs. A number of moths (Order: Lepidoptera; family Yponomeutidae) also spin large thick silk webs in which the larvae are concealed and protected. Another family, the Psychidae are called ‘bagworms’ because they make silk bags to hold the larvae and the wingless females. The larvae stick sand, twigs and leaves to the bags so that bags can be tough and difficult to tear apart, which gives the otherwise vulnerable larvae much needed protection. The most important insect silk spinner is of course, the silkworm moth, (family: Saturniidae). The last insect order that contains web spinners is the Hymenoptera (bees, wasps and ants) [15]

Morphological adaptations

Morphological adaptations include adaptations via various physical features which enable an insect to live a stress free life in adverse conditions. Morphological adaptations comprises mainly of (1) Mimicry (2) Camouflage**.**

Mimicry

Mimicry is the adaptive resemblance in signal between several species in a locality. The most spectacular and intriguing cases are of course those of accurate resemblance between distantly related species, such as spiders mimicking ants. Closely related animals can also benefit from mutual resemblance, in which case mimicry results from selection against signal divergence. Mimicry typically involves three players: two senders and one receiver. For mimicry to evolve it is essential that both senders benefit from eliciting the same response from the receiver. This provides the incentive for looking alike. Two situations can occur depending on whether it pays the receiver to react with a favored response towards only one of the senders or to both. Classical examples are Batesian and Mullerian mimicry. Both involve aposematic/warning signaling to a predator, and the favoured response is to not be attacked. In Batesian mimicry a palatable prey species mimics the appearance of another species noxious to predators thus reducing its risk of being attacked [16].

In Mullerian mimicry, two aposematic noxious forms conform to the same aposematic signal to their mutual benefit. In1879, German naturalist Fritz Muller was the first to develop a mathematical demonstration that two unpalatable prey could benefit from mutual resemblance. He found that, if the community of predators had to kill a certain (fixed) number of prey to learn to avoid them, two indistinguishable distasteful species would together suffer this mortality and both reduce their death rate per unit time. In Batesian mimicry, one of the sender species the mimic, sends a dishonest signal to deceive the receiver e.g., a predator. It is thought that deception is possible only if the receiver has previously inherited or acquired knowledge about this signal. The most famous Batesian mimic is probably the viceroy butterfly (*Limenitis archippus*) which mimics the monarch (*Danaus plexippus*). Hoverflies (Diptera: Syrphidae), diurnal moths (Sesiidae; Sphingidae), striped beetles (Cerambycidae) or crane flies (Tipulidae) are well known Batesian mimics of wasps and bees. Mullerian mimicry is common in *Heliconius* butterflies found throughout Latin America. Many of these species are members of mimicry complexes in which the same species takes on different mimitic patterns in different parts of its geographic range.

Camouflage

Camouflage is a protective strategy occurring in invertebrate lineages as diverse as sea urchins, gastropods, crabs and insects [17]. Animal camouflage, specifically in insects, has been studied extensively and has been a source of great fascination. Insects that look like their environment won't be seen by predators such as birds and lizards. Some insects look like sticks, leaves, and thorns. This type of adaptation helps insect survive by blending in with their surroundings so they aren't eaten or so that prey doesn't see them hiding. The mechanisms underlying camouflage vary greatly, from genetically programmed patterning of coloration that has proved valuable in survival [18].

The most famous examples of camouflage among insects are the specialized behaviors and associated morphologies in the larvae of green lacewings (family: Chrysopidae). Their campodeiform larvae are voracious predators generally living on trees, shrubs and plants in a wide variety of ecosystems and have been extensively studied as potential biological control agents in pest management programs [19]. These immature stages often exhibit camouflaging behavior, known as trash-carrying, in which they harvest plant materials or even detritus and carry them on their backs, nestled among cuticular processes specialized for the entanglement and transport of such debris. This trash packet camouflages the larva, preventing detection by predators and prey and constituting a defensive shield in instances where the larva is attacked [20].

Physiological adaptation

Physiological adaptation refers to internal mechanisms of insects to avoid unfavourable circumstances.

Adaptations to low temperature

Temperature is one of the most important abiotic factors in determining the state of activity and geographic distribution of organisms. Outside the lowland tropics and in temperate waters, temperature can decrease to below zero degrees on both seasonal and occasional basis. Such low temperatures are fundamental determinants of the life history of many ectothermic animals, of which insects form the overwhelmingly majority. To escape or alleviate low temperatures, insects have evolved a battery of physiological and behavioral strategies. For some species, behavior changes play a key role, such as the long distance migratory flights of monarch butterflies that allow them to escape winter altogether. Other insects escape to local shelters, for instance to thermally buffered microclimates that exist under the snow cover or within tree bark crevices. However spectacular long distance migrations are rare in insects, as is respite in warm local shelters. Thus, many species must still bear some of the brunt of low temperature exposure. A majority of insects that are subjected to seasonal temperatures that approach or exceed the freezing point of water have evolved a set of powerful physiological and molecular adaptations, collectively placed under the umbrella of "cold hardiness" to counter the effects of such stress. With respect to overwintering strategies, insects have traditionally been divided into two main groups: freeze tolerant and freeze avoiding, although this simple classification is underpinned by a complex of interacting processes, i.e. synthesis of ice nucleating agents, cryoprotectants, antifreeze proteins [21].

Freeze Avoidance

Freeze avoidance involves both physiological and biochemical mechanisms. One method of freeze avoidance is the selection of a dry hibernation site in which no ice nucleation from an external source can occur. Insects may also have a physical barrier such as a wax-coated cuticle that provides protection against external ice across the cuticle [22].The stage of development at which an insect over-winters varies across species, but can occur at any point of the life cycle (i.e., egg, pupa, larva, and adult). Freeze-avoidant insects (Table-1) that cannot tolerate the formation of ice within their bodily fluids need to implement strategies to depress the temperature at which their bodily fluids will freeze. Supercooling is the process by which water cools below its freezing point without changing phase into a solid, due to the lack of a nucleation source. Water requires a particle such as dust in order to crystallize and if no source of nucleation is introduced, water can cool down to -42°C without freezing [23]. In the initial phase of seasonal cold hardening, ice-nucleating agents (INAs) such as food particles, dust particles and bacteria in the gut or intracellular compartments of freeze avoidant insects have to be removed or inactivated. Removal of ice-nucleating material from the gut can be achieved by cessation of feeding, clearing the gut and removing lipoprotein ice nucleators (LPINs) from the heamolymph and in some species, by the shedding of the mid-gut during moulting [22]. In addition insects accumulate and synthesize cryoprotectants such as polyols and sugars, which reduce the lethal freezing temperature of the body. Although, polyols such as sorbitol, mannitol, and ethylene glycol can also be found, glycerol is by far the most common cryoprotectant and can be equivalent to ~20% of the total body mass. The depressive effect of glycerol on the super cooling point (SCP) is thought to be due to the high viscosity of glycerol solutions at low temperatures. This would inhibit INA activity [24] and SCPs would drop far below the environmental temperature. At colder temperatures (below 0°C), glycogen production is inhibited, and the breakdown of glycogen into glycerol is enhanced, resulting in increase in the glycerol levels in freeze avoidant insects (Table-1) reaching levels five times higher than those in freeze tolerant insects [25], which do not need to cope with extended periods of cold temperatures.

Though not all freeze avoidant insects produce polyols, all hibernating insects produce thermal hysteresis factors (THFs). A seasonal photoperiodic timing mechanism is responsible for increasing the antifreeze protein levels with concentrations reaching their highest in the winter. These antifreeze proteins are thought to stabilize SCPs by binding directly to the surface structures of the ice crystals themselves, diminishing crystal size and growth [24]. Therefore, instead of acting to change the biochemistry of the bodily fluids as seen with cryoprotectants, THFs act directly with the ice crystals by adsorbing to the developing crystals to inhibit their growth and reduce the chance of lethal freezing.

Freeze Tolerance

Freeze tolerance in insects refers to the ability of some insect species to survive ice formation within their tissues. All insects are ectothermic, which can make them vulnerable to freezing. Insects that have evolved freeze-tolerance strategies (Table-1) manage to avoid tissue damage by controlling extent of ice formation [26]. In contrast to freeze avoiding insects that are able to exist in cold conditions by supercooling, freeze tolerant organisms limit supercooling and initiate the freezing of their body fluids at relatively high temperatures. Physiologically, this is accomplished through inoculative freezing, the production of ice nucleating proteins, crystalloid compounds or microbes [27]. In order for a body of water to freeze, a nucleus must be present upon which an ice crystal can begin to grow. At low temperatures, nuclei may arise spontaneously from clusters of slow-moving water molecules. Alternatively, substances that facilitate the aggregation of water molecules can increase the probability that they will reach the critical size necessary for ice formation [28]. Freeze-tolerant insects are known to regulate the production of ice nucleating proteins that allows insects to control the formation of ice crystals within their bodies [27], for most freeze-tolerant insects it is important that they avoid supercooling and initiate ice formation at relatively warm temperatures [29]. This allows the insect to moderate the rate of ice growth, adjust more slowly to the mechanical and osmotic pressures imposed by ice formation. Nucleating proteins may be produced by the insect, or by microorganisms that have become associated with the insect tissues. The temperature that a particular ice nucleator initiates freezing varies from molecule to molecule. Although an organism may possess a number of different ice nucleating proteins, only those that initiate freezing at the highest temperature will catalyze an ice nucleation event. Once freezing is initiated, ice will spread throughout the insect's body [27]. Cryoprotectants play an important part in freeze tolerance (Table-1). The formation of ice in the extracellular fluid causes an overall movement of water out of cells, a phenomenon known as osmosis. As too much dehydration can be dangerous to cells, many insects possess high concentrations of solutes such as glycerol. Glycerol is a relatively polar molecule and therefore attracts water molecules, shifting the osmotic balance and holding some water inside the cells. As a result, cryoprotectants like glycerol decrease the amount of ice that forms outside of cells and reduce cellular dehydration [30].

Table 1: Supercooling points and Cryoprotectants reported for some Insects [31]

Species	Stage	Super cooling point (℃)	Cryoprotectant detected
Freezing Intolerant			
Rhabdophaga sp.	Larva	-62	Glycerol
Mayetiola rigidae	Larva	-58	Glycerol
Coccinella quinquenotata	Adult	-24	Glycerol
Papilio canadensis	Pupa	-27	Ethylene glycol
Freezing Tolerant			
Pytho americans	Larva	-7	Glycerol
Martyrhida ciniflorella	Adult	-23	Glycerol
Gynaephora groenlndica	Larva	-8	Glycerol, Alanine
Xylophagas sp.	Larva	-6	Glycerol
Rogas sp.	Adult	-30	Glycerol

Adaptation to Dryness

Many natural systems are seasonally dry, especially in summer and droughts can have significant and long term effects on ecosystems. Even many winter and summer habitats are very dry and adaptations to high temperature and dryness overlap. Several different adaptations enhance survival when water is in short supply, these adaptations serve to limit water loss, acquire water or tolerate water loss (Table-2).

Adaptations to high temperature

At the upper end of the temperature range above the preferred temperature, insects show a sharp rise in activity. At still higher temperature this is followed by an inability to move, a phase known as heat stupor and then by death. The temperature at which death occurs depends on the species, duration of exposure and interaction with other factors, in particular with humidity [25]. In response to high temperature insects show two types of acclimation recognised as: long term acclimation due to conditions during development and short term acclimation due to the immediate conditions, it is easily reversible. Short term acclimation is mainly due to production of heat shock proteins. These have been found in many insects as in *Drosophila* and *Locusta*, six heat shock proteins are found while in larvae of gypsy moth seven are reported [32].

Table 2: Mechanism of adaptation to dryness shown by insects [33]

Mechanism	Sample systems or substances
Limit loss	
Increase size	Larger insects have a lower surface/volume ratio and so loose water slowly
Reduce activity	Inactivity reduces respiratory loss
Seal cuticle	Additional or thicker wax coatings reduce cuticular permeability
Evolve modified spiracles	Sunken spiracles protected by hairs and other structures reduce water loss during respiration
Close spiracles	Spiracular closing inhibits spiracular water loss
Acquire water	
Drink	Normally only active individuals drink
Absorb liquid water	Some species have specific structures to absorb water, including egg hydropyles and the ventral tubes of spring tails
Absorb or condense water vapour	Some species have specific structural and physiological adaptations to extract water vapour from air
Tolerate loss	
Maintain high water content	Greater losses can be tolerated from a higher starting point
Survive low water content	Compartmentalizing water, regulating osmotic effects, making more water osmotically inactive
Enter anhydrobiosis	Metabolism ceases after a period of preparation, complex sequence of adaptations including protective substances, notably trehalose

Some expression of these proteins occurs at normal temperature, but expression is enhanced within seconds of a sharp rise in temperature [34]. At high temperatures, the proteins become denatured and clump together as insoluble aggregates. Heat shock proteins bind to surface of an aggregate and promote its dissolution, at the same time causes proteins to refold [35]. The first and foremost effect of temperature is on the evaporative water loss. Insects and other arthropods are particularly vulnerable, due to their relatively small size. Transpiration through the cuticle is the main route of water loss from insects, so physiologists have long been interested in cuticular mechanisms for water conservation [36]. The primary passive barrier to evaporative water loss is a thin layer of lipids on the surface of the cuticle. These lipids are highly diverse, sometimes including over 100 different compounds on a single individual [37]. The most widely accepted model is that the water-proofing abilities of cuticular lipids depend upon their physical properties, which depend in turn upon their chemical composition. A common observation (Fig. 2) has been that water loss from intact insects is relatively slow at moderate temperatures, then increases rapidly above a "critical" or "transition" temperature [38].

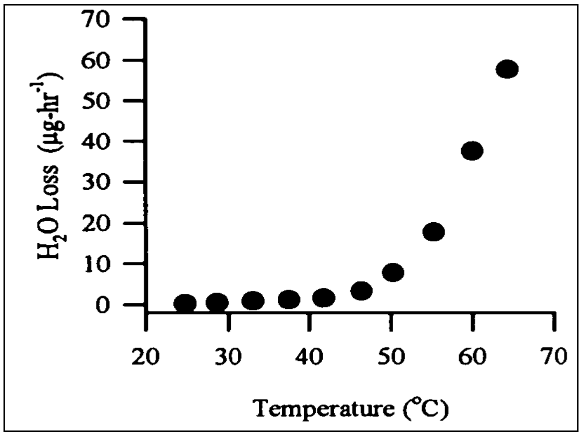
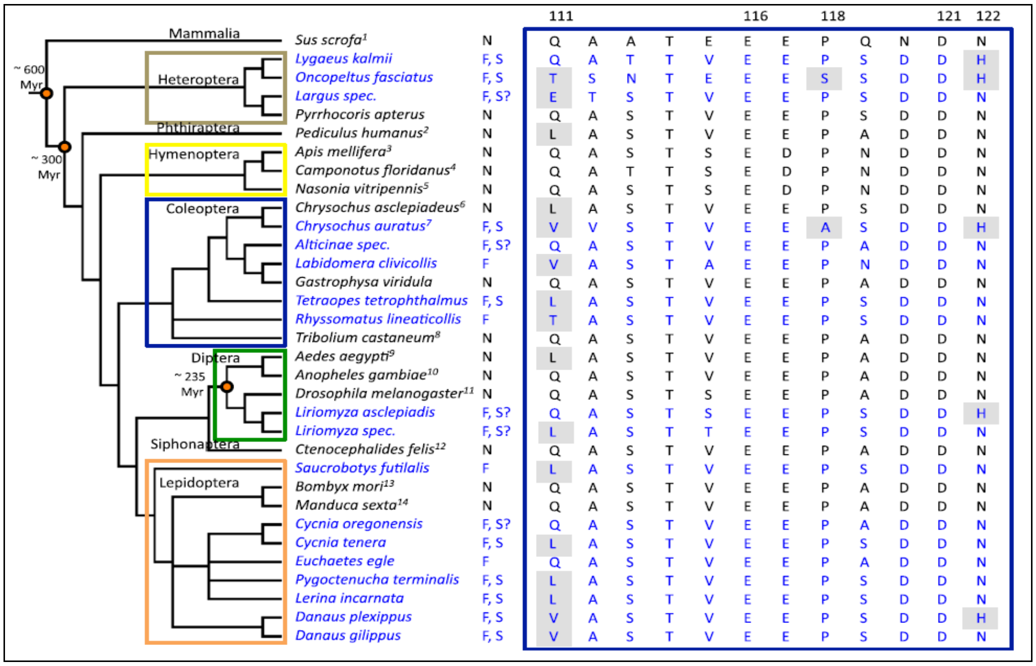


Fig 2: Effect of temperature on water loss from grasshopper *Melanoplus sanguinipes.*

Similar results have been obtained using excised patches of cuticle, indicating that this transition is due to a change in the permeability characteristics of the cuticle. Because of the importance of surface lipids in reducing cuticular permeability, it was suggested as early as that the transition in water loss rate is due to a change in the properties of the lipid layer. Specifically, it was hypothesized that surface lipids melt at the *Tc,* resulting in the conversion from a solid, impermeable barrier to a fluid state through which water can easily diffuse. Thus, the transition temperature (Fig. 2) for water loss would result from an actual phase transition of the cuticular lipids [39].

Adaptations to toxic cardenolides

The extent to which adaptive evolution is predictable at the molecular level is still highly debated [40]. When an evolution proceeds by alterations in genes of major effect, convergence at the molecular level is more likely than if many genes are involved [41]. Nonetheless, the genetic basis of adaptation is known only from a handful of organisms. The extent of convergent molecular evolution is largely unknown, yet is critical to understanding the genetics of adaptation. Target site insensitivity to cardenolides is a prime candidate for studying molecular convergence because herbivores in six orders of insects have specialized on these plant poisons, which gain their toxicity by blocking an essential transmembrane carrier, the sodium pump (Na,K-ATPase). On investigating the gene sequences of the Na,KATPase α-subunit in 18 insects feeding on cardenolide-containing plants (spanning 15 genera and four orders) to screen for amino acid substitutions that might lower sensitivity to cardendolides [42]. It was found that the replacement N122H that was previously shown to confer resistance in the monarch butterfly (*Danaus plexippus*) and *Chrysochus* leaf beetles was observed in four additional species, *Oncopeltus fasciatus* and *Lygaeus kalmii* (Heteroptera: Lygaeidae), *Labidomera clivicollis* (Coleoptera: Chrysomelidae) and *Liriomyza asclepiadis* (Diptera: Agromyzidae). Thus, across 300 million year of insect divergence, specialization on cardenolide containing plants resulted in molecular convergence for an adaptation likely involved in coevolution. Their screen revealed a number of other substitutions connected to cardenolide binding in mammals. Also it is confirmed that some of the particular substitutions provide resistance to cardenolides by introducing five distinct constructs of the *Drosophila melanogaster* gene into susceptible eukaryotic cells under an ouabain selection regime. These functional assays demonstrate that combined substitutions of Q111 and N122 are synergistic, with greater than twofold higher resistance than either substitution alone and >12-fold resistance over the wild type. Thus, even across deep phylogenetic branches, evolutionary degrees of freedom seem to be limited by physiological constraints, such that the same molecular substitutions confer adaptation. To address the convergence of molecular adaptation Dobler *et al.* 2012examined a diverse community of insect herbivores 18 species, representing deep phylogenetic divergences (Fig.3) specialized on plants that produce cardendolides (cardiac glycosides), a class of potent toxins that block Na,K-ATPase [42].



		111					116		118			121	122
Sus scrofa[1]	N	Q	A	A	T	E	E	E	P	Q	N	D	N
Lygaeus kalmii	F, S	Q	A	T	T	V	E	E	P	S	D	D	H
Oncopeltus fasciatus	F, S	T	S	N	T	E	E	E	S	S	D	D	H
Largus spec.	F, S?	E	T	S	T	V	E	E	P	S	D	D	N
Pyrrhocoris apterus	N	Q	A	S	T	V	E	E	P	S	D	D	N
Pediculus humanus[2]	N	L	A	S	T	V	E	E	P	A	D	D	N
Apis mellifera[3]	N	Q	A	S	T	S	E	D	P	N	D	D	N
Camponotus floridanus[4]	N	Q	A	T	T	S	E	D	P	N	D	D	N
Nasonia vitripennis[5]	N	Q	A	S	T	S	E	D	P	N	D	D	N
Chrysochus asclepiadeus[6]	N	L	A	S	T	V	E	E	P	S	D	D	N
Chrysochus auratus[7]	F, S	V	V	S	T	V	E	E	A	S	D	D	H
Alticinae spec.	F, S?	Q	A	S	T	V	E	E	P	A	D	D	N
Labidomera clivicollis	F	V	A	S	T	A	E	E	P	N	D	D	N
Gastrophysa viridula	N	Q	A	S	T	V	E	E	P	A	D	D	N
Tetraopes tetrophthalmus	F, S	L	A	S	T	V	E	E	P	S	D	D	N
Rhyssomatus lineaticollis	F	T	A	S	T	V	E	E	P	S	D	D	N
Tribolium castaneum[8]	N	Q	A	S	T	V	E	E	P	A	D	D	N
Aedes aegypti[9]	N	L	A	S	T	V	E	E	P	A	D	D	N
Anopheles gambiae[10]	N	Q	A	S	T	V	E	E	P	A	D	D	N
Drosophila melanogaster[11]	N	Q	A	S	T	S	E	E	P	A	D	D	N
Liriomyza asclepiadis	F, S?	Q	A	S	T	S	E	E	P	S	D	D	H
Liriomyza spec.	F, S?	L	A	S	T	T	E	E	P	S	D	D	N
Ctenocephalides felis[12]	N	Q	A	S	T	V	E	E	P	A	D	D	N
Saucrobotys futilalis	F	L	A	S	T	V	E	E	P	S	D	D	N
Bombyx mori[13]	N	Q	A	S	T	V	E	E	P	A	D	D	N
Manduca sexta[14]	N	Q	A	S	T	V	E	E	P	A	D	D	N
Cycnia oregonensis	F, S?	Q	A	S	T	V	E	E	P	A	D	D	N
Cycnia tenera	F, S	L	A	S	T	V	E	E	P	S	D	D	N
Euchaetes egle	F	Q	A	S	T	V	E	E	P	A	D	D	N
Pygoctenucha terminalis	F, S	L	A	S	T	V	E	E	P	S	D	D	N
Lerina incarnata	F, S	L	A	S	T	V	E	E	P	S	D	D	N
Danaus plexippus	F, S	V	A	S	T	V	E	E	P	S	D	D	H
Danaus gilippus	F, S	V	A	S	T	V	E	E	P	S	D	D	N

Fig 3: Community-wide convergent evolution in insect adaptation to toxic cardenolides by substitutions in the Na, K-ATPase [42]

Conclusion

Insects are adapted for life in every environment. They are found everywhere inhabiting marine, freshwater and terrestrial habitats from the equator to the poles. In order to survive the environmental extremes, to escape or alleviate adversities of environment, insects have evolved a number of physiological, behavioral and morphological changes or variations. These variations are governed by genetic characteristics and the well suited ones to environment are selected. These accumulated changes in them lead in to different types of adaptations. Thus it may be said that adaptations (physiological, behavioral and morphological adaptations) have played an important role in insects to become the most dominant organisms on the earth's surface. The widespread distribution of insects over many ecological niches is a testimony to their evolutionary success. Understanding adaptations requires a broad view of the effects temporal, spatial and resource patterns, key to the understanding of adaptations lies in the specific nature of environment. The responses of movement, habitat selection, defense, desiccation and resistance to cold, high temperature, food limitation all emerge from the selection pressures of the environment. Moreover, the extent to which adaptive evolution is predictable at the molecular level is still highly debated. The extent of convergent molecular evolution is largely unknown, yet is critical to understand the genetics of adaptation. However, the genetic basis of adaptation is known only from a handful of organisms.

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