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Susceptibility of *Drosophilids* in response to climate change

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Abstract
This review examines the impact of global warming in different *Drosophilid* species and other ectotherms. Global warming has been a hot topic since the rapid rise in average surface temperature of the earth over the last 3 – 4 decades. This rise in temperature/global warming is likely to have a major impact on all organisms living in earth's surface area. Ecothermic organisms like *Drosophilids* are likely to get more affect by this phenomenon. The effect of temperature on *Drosophilids* will be both genotypic and phenotypic. Phenotypic effects of temperature will lead to changes like melanisation pattern, shift in boundaries of species and change in phenology. Genotypic effects of temperature are also reported in recent studies which lead to chromosomal inversion polymorphisms in *Drosophilids*. Hence, many species which responds to change in temperature can be used as a good indicator to understand the impact of global warming and its effect on ectotherms surviving in various anthropogenic stressful environmental conditions. Such studies will also help us to establish better ecosystem conservation policies and might also change our research priorities in future.

Keywords: Climate change, shifting boundaries, melanisation patterns, thermal melanisation hypothesis, chromosomal inversion polymorphisms

Introduction

Ectotherms are susceptible to climate change because the environmental temperature heavily influences their fundamental physiological functions such as locomotion, development, and reproduction (Deutsch *et al*., 2008) [15]. The capacity of ectotherms for performing various physiological functions at different temperatures can be described by a thermal performance curve. The instantaneous effect of temperature on organism's fitness is marked by thermal performance curves which can later act as a framework for explaining the impact of fundamental components of global climate change. At mid to high latitudes, population growth rate rises suggesting increase in population fitness but in tropics it is anticipated that inherent population growth rates will decrease by up to 20 percent, suggesting that warming will significantly reduce fitness. On an average, the heat tolerance of tropical insects is around only one fifth of that of insects dwelling in mid-latitudes. Hence, the tropical insects will approach the near-lethal temperature sooner when compared to insects living on temperate climates although the tropical warming rate is said to be half when compared with high latitudes (IPCC, 2007).

Climate change and global warming

Global warming have an immense impact on plant and animal species which have led to noticeable modifications in their abundance, phenology, reproductive success, range size and range position from individual level to entire populations (Parmesan, 2006) [41]. Any living organism or a species might respond to rapid climate change by the following methods: (a) by changing the patterns of their distribution and abundance without evolving themselves, (b) by evolving themselves in combination with change in their distribution and abundance pattern or (c) they may get extinct. No distinct evolutionary reaction will occur against the climate change since species react individualistically to the environment. To add to this, every population also have their own limitations for tolerating physical variables, beyond which rapid extinction will follow. Therefore, the fundamental issue of organismal biologists is to study how climate change brings variations in organism's physiology, ecology and evolution (Brown *et al*., 1996; Chown & Nicolson, 2004) [7, 8].

Over the last century, there has been an extraordinary rise in the surface temperature of the earth of about 0.8˚C over the last 30 years i.e., approximately 0.2˚C increase per decade (Hansen *et al*., 2006) [19]. Such studies have demonstrated the occurrence of rapid change in the climate all around the world. Among the most basic effects of global warming is the disruption of the water cycle. It is a well-known fact that the rise in temperature will result in the increase in evaporation rate. Some species may exhibit increased resilience or adaptation to higher temperatures, while others may face decreased fitness and population decline (Hoffmann & Sgrò, 2011) [22]. Such changes in precipitation pattern will surely have a huge impact on various living organisms.

The evolutionary limits imposed by ecological traits, such as thermal tolerance and desiccation resistance, can constrain the ability of *Drosophilids* to adapt to climate change. Understanding these limits is essential for predicting the potential impacts of climate change on Drosophila species distributions (Hoffmann & Sgrò, 2011) [22]. Migration of different forest types towards the poles, drier deciduous forests and drastic change in crop type grown for food supply are some of the examples among the plant communities that is possible due to the effect of this climate change. Observed variations in phenotypic characteristics like the timing of life-history traits and geographic shift within the species range have proven that natural populations of an organism do respond to this climatic change. Most of the species have the capability to adapt and respond to global warming but such immediate adaptive response may also affect the genetic and chromosomal diversity at local level.

Previous studies observed that larval crowding induces the expression of heat shock protein 70 (Hsp70), which leads to increased adult longevity and enhanced resistance to thermal stress (Kellermann *et al*., 2009) [28]. HSPs play a vital role in cellular protection and facilitate acclimation to changing temperature conditions. These findings suggest that Drosophila species may have the capacity to adapt to changing environmental conditions, including those associated with climate change (Parmesan & Yohe, 2003) [40].

In ectothermic insects, melanisation patterns play a major role in their various ecological aspects (Majerus, 1998) [31]. The expression of phenotypic melanisation varies widely across different insect taxa. While Lepidopterans and Coleopterans displays both melanic and non-melanic morphs, certain *Drosophilids* can be characterised either through fixed or continuously varying patterns of body melanisation (True, 2003). The role of body melanisation patterns in maintaining the thermoregulation in ectotherms have been reported by many previous studies (Majerus, 1998; Rajpurohit *et al*., 2008b; Michie *et al*., 2011) [31]. Their field data have suggested that while darker morphs of alpine butterfly are more suited to higher altitude, the lighter ones are better suited for the foothills. In another study, darker patterns of body melanisation in wild ladybirds was produced at colder temperatures and the melanisation level increased with the length of time spent by pupal and larval stages at colder temperatures (Michie *et al*., 2011) [34]. There are other studies on the role body melanisation for pathogen resistance (Wilson *et al*., 2001; Dombeck & Jaenike, 2004) [53, 16] and resistance against various environmental stressors (Matute & Harris, 2012; Parkash *et al*., 2012) [38]. Furthermore, the impact of global warming on different *Drosophilids* and other ectothermic species have been summarized in Table 1.

Table 1: Various published data on effect of global warming in *Drosophilids* and other ectotherms

Study organism	Effect due to Global warming	References
Colias butterflies	Pigment polymorphisms	Watt, 1968
Drosophila flavopilosa	Seasonal fluctuations of the inversion polymorphism	Brncic 1972
Drosophila robusta	Genetic structure and change in natural populations	Etges 1984
Pieris butterflies	Wing melanisation patterns	Kingsolver, 1987
Drosophila melanogaster	Deleterious consequences of Hsp70 overexpression	Krebs and Feder 1997
Drosophila subobscura	Rapid micro-evolution and loss of chromosomal diversity	Rodríguez–Trelles & Rodríguez 1998
Eristalis arbustorum	Impact on abdominal pigmentation and fitness	Ottenheim et.al, 1999
Drosophila melanogaster	Reproductive costs of heat shock protein	Silbermann and Tatar 2000
Insect herbivores	Review on direct effects of rising temperature on insect herbivores	Bale *et al*., 2002
South African animal taxa	Range shift of species	Erasmus *et al*., 2002
Drosophila mediopunctata	Chromosomal inversion polymorphism	Ananina *et al*., 2004
Drosophila subobscura	Chromosomal inversion polymorphism	Balanya *et al* 2006, 2009
Terrestrial ectotherms	Impact on fitness	Deutsch et. al, 2008 [15]
Drosophila ananassae and *Drosophila nepalensis*	Shifting species boundaries of *drosophilids*	Rajpurohit *et al*., 2008a [43]
Drosophila ananassae	Effect on body color dimorphism and population	Parkash *et al* 2012 [38]
Drosophila melanogaster	Depletion of energy reserves	Klepsatel *et al*., 2016

Changes in species distribution and abundance as a result of climate warming

Anthropogenic climate change has disrupted the distributions and relative abundance of many species leading to loss or alteration of species habitat. Only few studies have tried to explain the relationship between the shifts in species distribution and the change in climatic conditions while investigating the shifting of species either towards the poles or towards higher altitudes (Rajpurohit *et al*., 2008a) [43] (Fig 1). This global warming is bound to have extreme and complicated impact on all species. Some of the probable and direct effects of global warming are categorized in the following:

Latitudinal and altitudinal distribution of species: With the rise in temperature the warmer climatic zone is bound to shift pole-ward and at higher altitudes which is definitely going to change the geographical range of all mobile species. Under such circumstances species in the montane regions will be most vulnerable to declining suitable habitat with the rise in altitude (Peters, 1985) [42]. Likewise, species in the lower altitudes or at the tropical regions suffer as they will have to move further at higher altitudes/latitudes proportionately for maintaining their climatic envelope.

Shift in movement patterns

With the rise in temperature, many species which currently migrate from one habitat to other might stop migrating since the migrating distance may either become too short or too long to travel making them year-round residents of that particular geographical region.

The abundance of species

The relative abundance of species will surely vary and reduce as a result of global warming. Such changes in the relative abundance will occur either through the direct impact on mortality or via less reproductive success in species due to climate change. Decreasing population size will ultimately reduce the genetic diversity of species. This global warming phenomenon might also interact with other survivability factors like precipitation and other processes in order to magnify its impact on the relative abundance of species.

Phenology Changes

Various life-cycle events influenced by the anthropogenic climate change can also separate the phenological relationships of species. *In situ* micro-evolutionary changes might occur in species have short generation period and high population growth rates.

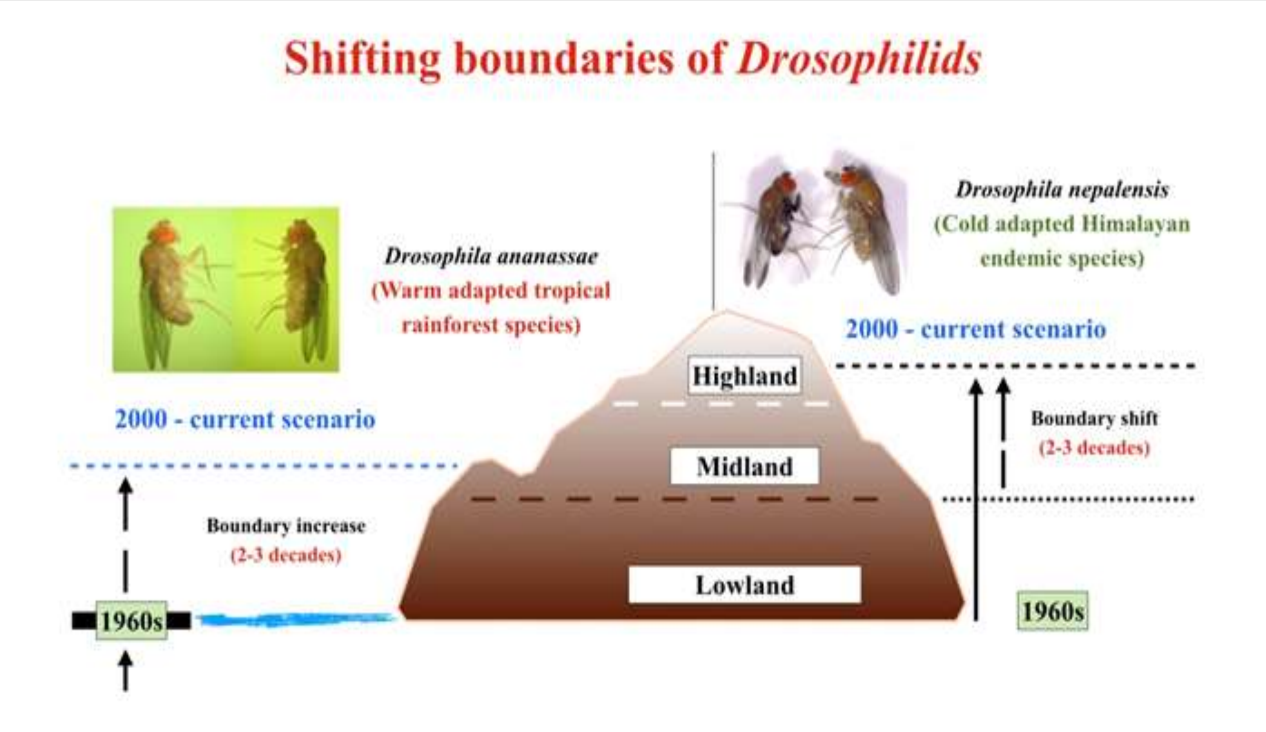

Fig 1: Schematic diagram representing "Shifting species boundaries of *Drosophilids*"

Impact of global warming - temperate versus tropical ectotherms

Most of the model organisms under organismal physiology have suggested that global warming will have a larger impact in the tropical region as compared to the temperate regions. The impact of climate change is not only measured by the extent to which the environmental temperature has shifted but also by observing/studying its effect on organism's behaviour, morphological, physiological and ecological aspects. Organisms having minimum acclimation capabilities and are specialized physiologically to temperature will experience the maximum impact of global warming. Individuals dwelling in a seasonal geographical region will also be at a higher risk to the effect of increasing earth's temperature. Janzen, in the 1960s had stated that ectotherms in the tropical regions are thermal specialists as they have minimum acclimation capabilities as compared to species in higher altitudes since they evolved in mostly constant and a seasonal geographical region.

Since the organisms living in the tropical regions experience a much warmer conditions throughout the year when compared with organisms in the temperate regions, a common understanding would be to consider that these tropical organisms are best suited to tolerate extreme heat stress. However, it may not be the case always since these tropical organisms are experiencing almost the same range of heat stress will less variation across all latitudes all the year round. In such environments, the organisms have already adapted and are surviving at close to or exceeding optimal temperatures and therefore, are left with hardly any behavioural alternatives to evade the rise in temperatures due to global warming.

Thermal safety margins

Thermal safety margin is a concept which attempts to describe the vulnerability of ectotherms due to climate change/global warming through macro physiological analyses (Deutsch *et al*., 2008; Sunday *et al*., 2014) [15, 50]. As mentioned earlier the organisms in tropical region are already surviving at physiological optimum temperatures and hence even a small rise in temperature will reduce its performance. It has been observed that ectotherms living at higher elevations and latitudes tend to have a larger thermal margins and greater heat tolerance limits (Sunday *et al*., 2014) [50]. It is due to this reason that a rise in temperature will boost the thermal performance of ectotherms living at mid to high latitudes as they are currently inhabiting cooler climates than optimum. In contrast, the tropical ectotherms will experience detrimental impacts of global warming. Such phenomenon is relevant to both the ectotherms as well as terrestrial vertebrates. Hence, heat tolerance and thermal safety margins can become useful indicators for better understanding of climate change/global warming. If the earth's surface temperature continues to rise in future, then the only way to attenuate its impact on ectotherms will be through acclimation, adaptation, dispersal and behavioural plasticity (Deutsch *et al*., 2008) [15]. Under such circumstances, the tropical ectotherms will be at a higher risk of extinction due to global warming when compared with temperate ectotherms living at higher elevations and latitudes.

Plastic responses to environmental stress

Plastic responses to environmental variability can provide fast and efficient means to deal with thermal stress, including rapid hardening and acclimation, among others.

Under various environmental conditions when one genotype is able to express multiple phenotypes it is known as phenotypic plasticity (Bradshaw, 1965) [6], it can play a significant role in insect responses to climate change, including *Drosophilids*. It can be calculated as a slope of reaction norm (De Jong, 1990) [14]. Plasticity in traits such as thermal tolerance and development rate can provide a buffer against the impacts of changing climatic conditions (Reed *et al*., 2011) [46]. However, the extent and limits of plasticity vary among species, the limits and adaptive potential of plasticity require further investigation to accurately predict the responses of *Drosophilids* to climate change. This plasticity can be both adaptive and non-adaptive. Adaptive plasticity may occur when it is able to improve the fitness of ectotherms as compared to those who are non-plastic whereas non-adaptive plasticity is a result of passive response to varying climatic conditions. It is complicated to understand how climatic variation can change trait's plasticity since the adaptive value of plasticity varies for fitness and non-fitness traits. In *Drosophilids*, fitness traits like fecundity, ovariole number and size also get affected by environmental changes (Bergland *et al*., 2008) [5].

Thermal acclimation of Drosophilids

Temperature is considered to be one among the most significant environmental factors which dictates the survival and dispersal of ectotherms because almost all the biochemical and physiological processes are affected by the ambient temperature (Cossins, 2012) [10]. The same is also implied to other ectothermic and endothermic insects whose behaviour, physiology and biochemical adaptive range have evolved for withstanding exposures to severe seasonal and thermal fluctuations. Generally, the cold-tolerant ectotherms are defined as freeze-resistant/freeze-avoiding but in real time most of these individuals die before reaching the body fluid's crystallization temperatures. At lower temperatures such individuals have no tolerance at all (Sinclair *et al*., 2003) [49].

For an example, *Drosophila melanogaster* a fruit fly is susceptible to chilling injuries at temperatures which are above the freezing point (Czajka & Lee, 1990) [11]. When *D. melanogaster* was acclimated at lower temperatures, there was an increase in the levels of ethanolamine which were more than 50% but at the expense of choline present in the glycerophospholipids (GPLs). As the acclimatization temperatures in these flies were reduced there were small changes in the molecular composition of lipids which were statistically significant (Overgaard *et al*., 2008) [36]. Threefold decrease in the level of epicuticular lipids in both larval and adult stages of *Drosophila simulans* when grown at 25˚C in comparison with flies grown at 15˚C has also been reported previously (Parkash *et al*., 2013) [37]. Acclimation of *D. melanogaster* at non-lethal climatic stressors also improved their desiccation and heat resistance (Kristensen *et al*., 2008) [30]. Further when these flies were subjected to cold acclimation it improved the lifespan of flies but the mortality and recovery rate after sub-zero temperature exposure was decreased (Rako & Hoffmann, 2006) [45]. Reproductive and energetic costs in *Drosophila melanogaster* as a result of both heat acclimation and heat shock have been reported in previous studies (Silbermann & Tatar, 2000) [48].

Role of pigmentation in thermoregulation, starvation resistance, desiccation resistance

Ectothermic species are susceptible to the circumstances of temperature in which they can function. In nature since temperature varies in a spatiotemporal manner each day, the ectothermic species have to come up with multiple strategies to survive under these environmental conditions at the local level. This is crucial for small insects as an insect which weighs around 10 mg can increase their body temperature by 10˚C under just 10 seconds when approaching direct sunlight (Heinrich, 1993) [20]. This is an even more serious concern for *Drosophilids* whose body weight is hardly 1-2 mg. Here melanism has a significant role to play in insect thermal ecology (Trullas *et al*., 2007) [52]. Hence, melanin has received worldwide attention for its role in thermoregulation (Fig 1). A darker cuticle can avail various physical properties (Kalmus, 1941; Majerus, 1998; True, 2003) [27, 31, 51]. Dark morphs are believed to be result of the capacity to absorb heat more easily than light flies, with darker phenotypes benefiting from cooler climates (Gibert *et al*., 1996) [18]. Melanism in ectotherms exhibits a large amount of variability and this could result from genetic polymorphism or phenotypic plasticity. On the thorax (trident dark shape pattern) and abdominal sections, body pigmentation can be evaluated (David *et al*., 1990) [12]. Such differences occur either through plasticity or genetic polymorphism. While performing physiological assays in the laboratory, there was a significant increase in the internal temperature of dark trident flies when exposed to solar radiation. At the same time the cuticular toughness was also enhanced by beta-alanine, an amino acid that is responsible for cuticular tanning (not dark pigment) (Jacobs, 1985) [25].

In the dark pigmented insects the melanisation present in the wings also helps them to increase body temperature to optimum for daily activities as compared to their lighter counterparts by absorbing solar radiations (Ottenheim *et al*., 1999) [35]. A darker cuticle can enhance solar absorption during the cold season in temperate regions, which improves the fly's thermal balance. Simultaneously, lighter cuticles in tropical countries can decrease light absorption (Gibert *et al*., 1996) [18]. It would therefore be predicted that a phenotype's overall pigmentation is related to fitness.

Thermal melanisation hypothesis

It is a common fact that dark surfaces tends to absorb and radiate more heat as compared to lighter surfaces. Similarly, dark melanic ectotherms increase their body temperature faster than the lighter or non-melanic ectotherms. This co-evolution phenomenon forms the basis of "Thermal melanisation hypothesis" (Fig. 2) in ectothermic organisms (Angilletta, 2009) [3]. Such co-adaptation of traits between body pigmentation and heat resistance are also shown by *Drosophila melanogaster* (Parkash *et al*., 2010) [39].

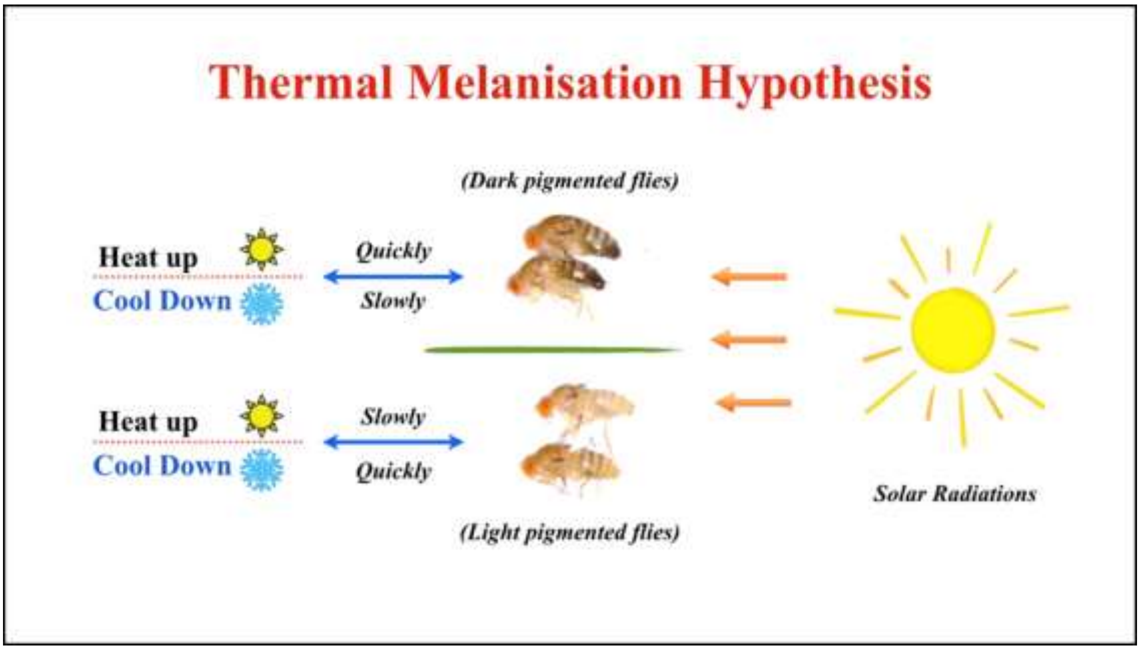

Fig 2: Schematic diagram representing "Thermal melanisation hypothesis".

Water conservation in the context of global climate change

Water is major constituent (~70%) in almost all organisms and their survivability depends on how they are able to maintain this water balance. Maintaining water balance is a great challenge for insects. Therefore, they have developed multiple strategies for survival under drought conditions. Major focus has been on the study of effect of global warming on living organisms (Helmuth *et al*., 2010) [21]. Similar attention is also required for the varying patterns of rainfall, relative humidity and water availability since all these factors are affected by the rise in global temperature. Change in precipitation has extreme on all organisms be it animals (Jetz & Rubsenstein, 2011) or insects (Wolda, 1988) [54]. Sometimes in many species precipitation defines their range position (Roura-Pascual *et al*., 2011) [47]. Since optimum thermal temperature is highly related with ambient precipitation rather than average ambient temperature, species richness can also be correlated with precipitation at the local level (Roura- Pascual *et al*., 2011; Clusella-Trullas *et al*., 2011) [47, 9].

The current scenario of global warming involves direct (Fung *et al*., 2011) and indirect effects on both precipitation and water availability (Makarieva & Gorshkov, 2007) [32]. Therefore, in the context of global climate change there is an utmost need to study the physiological mechanisms of insects and their ability to cope against drought stress through multiple strategies.

Depletion of energy reserves in drosophilids during global warming

Exothermic organisms not only face the problems of adapting to the rising mean temperature but also to higher fluctuations of short-term temperatures (Hoffmann *et al*., 2013) [23]. Hence, for understanding the impact of global warming on ectothermic organisms it is necessary to study how metabolic and physiological mechanism of such organisms are affected by the environmental temperature. Klepsatel *et al*., 2016 [29] studied the impact of thermal stress in energy reserves of ectotherms. In their study, when different strains of laboratory and wild populations of *Drosophila melanogaster* were subjected to thermal stress, it had a lasting memory effect on body fat reserves. Thermal stress further triggered a stress-induced cellular response i.e., the activation of heat shock proteins (Hsps). In their study they observed that under extreme thermal stress, cellular response might also cause cell apoptosis including the fat body cells which will further have an irreversible impact on fat storage capacity of these flies. Overall, the study proved that thermal stress/global warming can have a significant negative impact on the fitness of ectotherms.

In several other studies it was observed that the expression of Hsps under thermal stress reduced the growth, hatchability, juvenile viability and age-specific mortality of *drosophilids* (Silbermann & Tatar, 2000) [48]. Such studies suggests that anthropogenic global warming might cause an antagonistic pleiotropy phenomenon in an ectothermic organism.

Micro-evolution and Global genetic change in Drosophilids in response to global warming

Many studies have presumed that the global climate change will result in primary shift in geographical boundaries of species and have corresponding focus on population movements at species borders (Parmesan, 1996; Rajpurohit *et al*., 2008a) [43] with minimum or no impact in genotype or phenotype. Even though scientists claims that global warming will only affect the species distribution (Parmesan, 1996), very few have considered the micro-evolutionary changes that may arise in combination with boundary shifts. Since we have little knowledge of these micro-evolutionary processes while migration capacity and frequency of every species vary from one to another (Davis, 1981) [13], it is vital to study both the demographic and evolutionary processes.

In *Drosophilids* polytene chromosome inversions was discovered as early as 1936 by Sturtevant and Dobzhansky. Since then seasonal chromosomal inversion polymorphism has been studied by many researchers (Ananina *et al*., 2004) [2] and they have provided some detailed information about evolutionary change. But the work in *Drosophila subobscura* (Balanya *et al*., 2006) have provided us the conclusive evidence that *Drosophilids* can act as a good indicator to study microevolutionary changes as a result of climate change. These studies in *Drosophila subobscura* suggest that temperature has a significant genetic impact in ectothermic organisms which is vivid through major chromosomal inversion polymorphisms present in these flies distributed over three different continents (Balanya *et al*., 2006). As of now the underlying mechanisms of these changes is not well understood but even then the genetic changes occurring in *Drosophilids* can be used as an effective tool in tracking global warming and its impact on ectotherms worldwide.

In summary, a holistic method of study considering the changes in plasticity, energy metabolites and chromosomal inversion polymorphisms in *Drosophila* species would help us better to understand the impact of global warming and its effect on ectotherms surviving in various anthropogenic stressful environmental conditions. Such studies will also help us to establish better ecosystem conservation policies and might also change our research priorities in future. The paper concludes that climate change poses significant challenges to species, including *drosophilids*, and their ability to adapt through evolutionary processes.

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