



VARIATIONS IN THE BIOLOGICAL AND ECOLOGICAL ATTRIBUTES OF INSECTS DUE TO CLIMATE CHANGE: A REVIEW

K CHANDRAKUMARA¹, ASHOK KUMAR SAU^{1*}, ANKUR², RAJESH¹,
ADITYA K TANWAR¹ AND BASAVARAJ N HADIMANI¹

¹Division of Entomology ICAR, Indian Agricultural Research Institute, New Delhi 110012, India

²Department of Entomology, Maharana Pratap University of Agriculture and Technology,
Udaipur 313001, Rajasthan, India

*Email: aksahulks@gmail.com (corresponding author): ORCID ID 0000-0003-1221-1932

ABSTRACT

Climate change is causing a shift in long-term weather patterns and altering parameters such as temperature, atmospheric CO₂, and precipitation patterns. It is likely to be an indirect effect of greenhouse gases and their enhancement in the atmosphere largely induced by human activities. As poikilothermic animals, insects are highly dependent on environmental conditions, particularly temperature, which affects various aspects of their life. Climate change have a direct impact on insect pests by affecting their population dynamics, diurnal activity, growth rate and diapause. It may lead to a range expansion, increased overwintering survival, more generations per year, elevated risk of invasive insect species and insect-borne plant diseases, and changes in their interactions with host plants and natural predators. Indirectly, changes in climate can modify host plants and competitors, further complicating the effect on insect biology and phenology. Impact of elevated CO₂ levels on their host plants can affect growth rates, fecundity, and population densities of insects. Altered precipitation patterns, such as droughts and floods, affect insect survival and diapause. Further, there is significant implications of climate change on different aspects of insect ecology, including insect distribution, behavior, and communication. The climate changes are predicted to alter the geographic ranges and migration behavior of insect species, creating new ecological niches and removing low-temperature barriers. These changes can threaten food security and increase the latitudinal and altitudinal range of crop pests. It also affects natural enemies, which can decrease the plant defense system against insect pests. Additionally, climate change can affect pheromonal communication, including production to behavioral response, in insects that rely on long-range chemical signals for communication. The review paper highlights the potential impacts of climate change on insect biological, phenological and ecological aspects.

Key words: Global warming, climate change, GHG, Temperature, precipitation, CO₂, diapause, population dynamics, voltinism, phenology, distribution, chemical ecology, pheromone communication, insect pests

Climate change refers to a gradual shift in the long-term patterns of weather in a particular area. It involves a range of parameters such as an increase in temperatures, atmospheric CO₂ levels, and changing precipitation patterns. The rise in temperatures, increased CO₂ and other greenhouse gases, and altered precipitation patterns are causing climate extremes, which are a serious threat to global food production (Shrestha, 2019). Mean temperature has been increasing as a result of ongoing climate change and is predicted to rise by 1.5°C within the next two decades than preindustrial levels (the average over the years 1850-1900) (IPCC, 2022). It is suggested that the average temperature may increase by 1.7–5.3°C as a result of increasing greenhouse gases (CH₄, CO₂, and N₂O) concentration within the coming 60-100 years (IPCC, 2022; IPCC, 2014). The agriculture sector is responsible

for approximately 21% of global GHG emissions (Lamb et al., 2021), with significant variability worldwide. By 2030, greenhouse gas emissions are expected to rise nearly 40%, mainly through direct emission as CH₄ and N₂O or indirectly in the form of energy consumption by the agricultural system (CO₂) (Vermeulen et al., 2012). The complexity of climate change is evident in the fact that night-time temperatures are warming faster than day-time temperatures across much of the planet, as study on warming from 1983 to 2017 found a difference in mean annual temperature of more than 0.25°C between daytime and night-time warming (Cox et al., 2020; Speights et al., 2017).

Insects are cold-blooded animals whose body temperature varies with that of the surrounding environment. Therefore, insects are highly dependent

on the thermal conditions of their environment which influences various aspects of their life (Kocmankova et al., 2010). Climate conditions are one of the primary factors that determine insect distribution ranges, along with food plants. Climate change is affecting the distribution and severity of crop pests (Macfadyen et al., 2018; Lamichhane et al., 2015), with regions at higher latitudes facing severe increases that could disproportionately impact insects (Bale and Hayward, 2010). So, climate change is likely to have a significant impact on insect pests, posing a serious threat to sustainable food production (Andrew and Terblanche, 2013). Predicting the impacts of climate change on insect pests is challenging due to the complex interactions of increasing atmospheric CO₂ concentration, changing climatic regimes, and altered intensity/frequency of extreme weather events (Bebber et al., 2013; Gregory et al., 2009). Climate change can also indirectly affect insects through the differing responses of host plants and natural enemies of insect pests. Further, different thermal preferences for insect pests and their natural enemies can negatively affect the synchronization between them and cause a risk of pest outbreaks (Furlong and Zalucki, 2017; Hance et al., 2007).

Agricultural research is focused on understanding the impacts of climate change and associated phenomena on agricultural production and agricultural insect pests. Temperature rise directly affects the survival, reproduction, spread, and population dynamics of the pest, as well as the relationships between pests, the environment, and natural enemies (Prakash et al., 2014). This review provides an overview of the possible effects of climate change on insects in various ways. Here the impact of some of the predicted climate changes, especially the increase in temperatures and atmospheric carbon dioxide concentrations along with changing precipitation patterns on the biology, phenology, ecology, and physiology of insects, especially agricultural pest species is reviewed.

Response of insects to rising temperatures, CO₂ and changes in precipitation

Insects are known to be highly adaptable organisms that respond differently to various impacts of climate change (Skendžić et al., 2021). The physiology of insects is highly sensitive to temperature fluctuations (Dukes et al., 2009). With temperature being the most crucial environmental factor affecting the dynamics of insect populations by altering fertility, it is anticipated that a warming climate could lead to a range expansion,

increased overwintering survival, more generations per year, an elevated risk of invasive insect species and insect-borne plant diseases, as well as changes in their interactions with host plants and natural predators (Skendžić et al., 2021; Bale et al., 2002). It can accelerate insect consumption, development, and mobility, and overall population size (Bale et al., 2002). Species that can adapt to changing temperatures will thrive, while those that cannot will decline. The rising CO₂ level has various impacts on insects, mainly by affecting their host plants. Elevated atmospheric CO₂ levels can impact the distribution, abundance, and overall performance of herbivory. Such changes may affect the consumption rates, growth rates, fecundity, and population densities of insect pests (Fuhrer, 2003). The feeding response of herbivory is also likely to be uneven on C₃ and C₄ plants (Lincoln et al., 1984). Elevated CO₂ levels can alter the nutritional quality and palatability of leaves, affecting the leaf-feeding insects' consumption and survival (Lincoln, 1993). Due to climate change, precipitation patterns have altered, with decreased frequency and increased intensity. This change has favored the incidence of droughts and floods, affecting insect survival and diapause (Shrestha, 2019). During severe rainfall, small-bodied insects like jassids, aphids, mites, and whiteflies can be washed away (Pathak et al., 2012).

Impact of climate change on biology and phenology of insects

Climate change and weather alterations have significant impacts on the biology and phenology of insect pests. As generally adaptable organisms, insect pests respond differently to different factors of climate change (Skendžić et al., 2021). These changes affect insect population dynamics, diurnal activity, growth rate, reproduction, winter performance, and diapause in complex ways. They also indirectly impact insects by modifying their host plants and competitors (Bale et al., 2002). Furthermore, research suggests that tropical insects are more vulnerable to warming situations because tropical areas have experienced less climatic variability historically, and insects in these regions are already closer to detrimental thermal maxima than temperate insects (Garcia-Robledo et al., 2016; Deutsch et al., 2008). Insect pests are impacted directly and indirectly by climate change. Direct effects include changes to the pests' biology, phenology, and distribution, while indirect effects involve modifications to the host plant on which they feed, as well as interactions with natural enemies, other insect species,

competitors, and the environment (Prakash et al., 2014). Although it is challenging to predict the precise effect of climate change on insect biology and phenology, different species respond differently to climatic variation even within the same landscape (Nice et al., 2019). Nonetheless, if the changes in environmental factors are observed in isolation, the following impacts on insect biology and phenology can be identified.

Population dynamics and voltinism

An increase in average temperature can accelerate the growth and reproduction of insect species, resulting in shorter life cycles and higher numbers of larvae on a single host plant, as well as an increased frequency of outbreaks (Jönsson et al., 2007). This change in population dynamics due to climate change is likely to escalate the population size and pest activities in many insect groups (Puri and Ramamurthy, 2009). Temperature changes can also affect the survival and development rates of insects, as well as their voltinism (the number of generations produced in a year), which can impact population density, size, and genetic composition, as well as the level of damage inflicted on host plants (Bale et al., 2002). The population model of the grape berry moth, *Paralobesia viteana*, predicts that a temperature increase of more than 2°C can have a significant impact on its voltinism, causing a shift in the timing of its ovipositional period that is currently controlled by photoperiod-induced diapause (Tobin et al., 2008). Under current climate conditions in Brazil, the voltinism of *Spodoptera eridania* as reported to range from 2.9 to 9.2 generations, with fewer cohorts in low temperature regions and more in warmer ones, and a considerable increase in the number of generations of *S. eridania* was projected under climate change scenarios (Sampaio et al., 2021). In one of the study from India, with mean temperature is predicted to increase by 0.51°C, 1.03°C, 1.57°C and 2.1°C in climate years 2030, 2050, 2070 and 2090, escalated annual *Helicoverpa armigera* generation to 12.9, 13.3, 13.8 and 14.2, respectively. There will be 3-12% increase in *H. armigera* generations in future climate years in India (Bapatla et al., 2022).

Diurnal activity response and insect phenology

One of the most well-known effects of recent global warming is alterations in phenology, or the timing of seasonal lifecycle events (Radchuk et al., 2019; Thackeray et al., 2016; Menéndez, 2007). Many species are now appearing earlier in the spring and remaining active for longer periods, which can have significant

impacts on population dynamics and abundance (Macgregor et al., 2019; Roy et al., 2015). As host plant phenology is also affected by climate change, insects must rapidly adapt their phenology to synchronize with these critical resources for survival and fitness (Van Asch et al., 2013; Van Asch et al., 2007). However, if microclimate temperatures become too warm for insects to feed and forage, they may alter their behavior and activity patterns to avoid these conditions, which can be challenging depending on the species' level of plasticity in their responses to temperatures and photoperiod, as well as any ecological interactions that may limit their ability to adapt (Andrew and Terblanche, 2013).

Growth rate, reproduction and abundance

The response of insects to rising temperatures can be positive, such as increased reproductive potential, as long as species growth maxima are not surpassed. As ambient temperatures generally increase toward optimal temperatures for growth and development of many insect species, possibly reducing thermal constraints on population dynamics, the abundance of insects expected to increase under global warming scenarios (Skendžić et al., 2021). Higher CO₂ levels cause changes in the C: N ratio of plants, leading to an increase in the consumption of plants by insect pests, as nitrogen is essential for insect growth (Bezemer et al., 1998). This increased consumption can result in greater plant damage, as insect need to consume more plant tissue to obtain the same energy. When nitrogen levels drop, as expected due to CO₂ fertilisation, leaf feeders increase their consumption rates to compensate nutrient deficiency (DeLucia et al., 2008; Hamilton et al., 2005). Under increased temperature conditions, the egg, larva, and pupal stages' developmental periods shorten, as demonstrated by Karolewski et al. (2007) that the growth period of the gypsy moth *Lymantria dispar* (L.) was significantly reduced in their laboratory experiment as a result of an increase in temperature. Warmer weather shortens the life cycle of insects, resulting large number of generations and faster life histories. This causes more generations in a cropping season and can aggravate the pest complex (Puri and Ramamurthy, 2009). This quicker development means shorter exposure to adverse conditions such as low temperatures, parasitoid attacks, predator attacks, and entomopathogens. This shorter exposure can lead to the reproductive success of many insect species. However, crossing a specific optimum temperature range can reduce growth rates, fecundity, and increase mortality rates for many species (Rouault et al., 2006).

Increased overwinter survivability and winter performance

Insects face a significant challenge in overwintering in temperate regions, as highlighted by Williams et al. (2015). With climate change, winters are anticipated to become more variable in addition to warmer. The severity of cold stress is determined by extremely low temperatures, which disrupt ion balance in crucial tissues, leading to membrane depolarization and eventually programmed cell death and chilling injury (Bayley et al., 2018; Overgaard and MacMillan, 2017). Crossing the minimum threshold temperature has been shown to have additional energetic and fitness costs for insects (Marshall and Sinclair, 2018). So, warming of winter may lead to higher winter survival in insect due to lower survival cost. Furthermore, increased mean temperatures during the winter can cause energy depletion for insects unable to feed during this time, leading to decreased fitness (Sinclair, 2015). So, winter performance may have mixed performance in difference species based on their adaptation strategy and cold hardiness mechanism.

Diapause

Insects have developed several survival strategies to overcome unfavorable winter conditions, including diapause, a dormant period during which an insect's metabolic and physiological processes are slowed down. In temperate insects, the initiation and termination of winter diapause are critical life-history changes that regulate the time spent on development and population growth (Kostal, 2006). Several studies have shown local adaptation in the timing of diapause in both insect pests and natural enemies (Lindestad et al., 2019; Posledovich et al., 2015; Paolucci et al., 2013), indicating that they may evolve in response to changing climate conditions (Bradshaw et al., 2001). Studies on genome-wide association suggest that local adaptation in diapause induction and termination timing is linked to variation in circadian clock genes of insects (Kozak et al., 2019; Pruijscher et al., 2018). Typically, short day lengths at the end of the growing season and the beginning of harsh winter conditions are used as a cue for diapause induction (Lindestad et al., 2019; Kostal, 2006; Hodek, 1996). However, the adaptive value of photoperiodic induction relies on historical relationships between photoperiod and specific value of climatic variables such as temperature and rainfall. Rapid climate change can distort these correlations, leading to unsuitable diapause timing (Kerr et al., 2020; Van Dyck et al., 2015). Additionally, the timing of

diapause termination and subsequent spring phenology is generally affected by temperature during winter (Lehmann et al., 2017; Kostal, 2006; Hodek, 1996). Therefore, climate change can impact diapause patterns and spring phenology in complex ways, altering the phenological synchronization to essential resources and enemies, thus affecting both ecological and evolutionary processes in insect populations (Kharouba et al., 2018; Forrest, 2016).

Impact on insect ecology

Climate change is expected to have a significant implication for different aspects of insect ecology. It can create favorable conditions for pests to thrive and expand their range. Insects have distinct life stages that can vary in their responses to environmental factors (Kingsolver et al., 2020). Some pests, which are currently restricted to small areas or low densities, may be able to exploit the changing conditions and distribute more widely, leading to damaging population densities (Bale et al., 2002; Porter et al., 1991). Climate change can also affect the synchronization within and between insect species. Even though parasitoids respond to climate change in similar ways to herbivores, their close relationship with their hosts and their particular life cycle make host-parasitoid synchrony and population cycles challenging under changing climate (Tougeron et al., 2020). Insect communication, which relies on volatile compounds, may also be impacted by changes in temperature and humidity. These changes can affect the production, release, and detection of these compounds, thereby altering the behavior and survival of insects. Understanding these potential impacts is also important for developing effective strategies to control insect pest.

Distribution: Geographic range expansion and migration behaviour

The extent and range of occurrence of an insect species is very much influenced by the climate of a region (Ramamurthy, 2009). So, unfavourable climate is one of the factors that decides the boundary for the distribution of a particular insect species. Insects have species-specific climatic requirements that are crucial for their development and survival. Climate change may have a significant effect on the geographic distribution of insect species, and low temperatures are often more critical in determining their geographic range than high temperatures (Skendžić et al., 2021). Upper latitudinal margins limit the distribution of a species due to relatively cool climate (Ramamurthy,

2009). Insect species are moving towards polar areas whose expansions were previously restricted by acute low temperatures, and the range boundary is determined by climate extremes rather than mean temperatures (Lynch et al., 2014; Battisti et al., 2005). Northern and southern range shifts are predicted for many insect species towards higher altitudes and elevations (Menéndez, 2007; Parmesan and Yohe, 2003). Many of the species expanding their geographic range are thermal generalists, and their expansions are driven by declined winter mortality (Lancaster et al., 2016). Predicted changes in temperature, CO₂, and precipitation patterns resulting from climate change will influence the distribution, geographic ranges, and migration behavior of insect species (Fand et al., 2012). These changes may create new ecological niches and remove low-temperature barriers, providing opportunities for insect pests to spread across physical and political boundaries, threatening food security (FAO, 2008). Climate change and the resulting changes in land use are expected to cause an overall global pattern of increasing latitudinal and altitudinal range of crop pests (Barzman et al., 2015; Gregory et al., 2009). Over longer timescales, insect species in their current habitat may respond to changing climates in various ways. They may adapt to new climatic conditions in their existing habitats through genetic, physiological, or behavioral changes. Alternatively, they may adapt to new climatic conditions in their present range while simultaneously extending their range to remain within their current climatic envelope. Populations may also not adapt to the changing local climatic situations and shift their range entirely to stay within their optimal climatic envelope or go locally extinct, leading to the population's eventual extinction (Andrew and Terblanche, 2013). The ability of a species to respond to the increasing temperature and expand its range will depend on number of life history characteristics, making the possible response quite variable among species (Subrahmanyam et al., 2009).

Tritrophic (interspecific) interaction and chemical Ecology

Climate change is changing ecosystems by altering composition of communities, and trophic interactions. Climate change can increase exposure to heat stress and result in phenological and morphological mismatches with adjacent trophic levels (Abarca and Spahn, 2021). Increasing temperatures and CO₂ have a profound impact on the insect physiology which in turn, can have significant consequences on interactions between crops and herbivores (Caulfield and Bunce, 1994). As

climate change alters plant phenology, it also affects the growth and abundance of herbivores feeding on these plants, which consequently affects natural enemies by altering their availability of prey and hosts. Due to changes in plant phenology, there may be a reduction in predation and parasitism by natural enemies, since an increase in plant foliage and variations in herbivore life cycle can have a significant impact on their availability as prey (Coviella and Trumble, 1999). Changes in flowering and growth pattern of host plant due to climate change can create a serious imbalance in insect host plant relationships and their tri-trophic interactions (Puri and Ramamurthy, 2009). While changing synchrony with their host plant, insect same time adapting to the climate variables (Ramamurthy, 2009). Further, numerous studies conducted in a controlled environment have shown that changes in temperature, CO₂, precipitation, relative humidity, and other environmental factors can alter the production of secondary metabolites and defensive traits of host plants, which can have a considerable effect on insect-plant interactions (DeLucia et al., 2012; Zavala et al., 2008; Zvereva and Kozlov, 2006). These changes can decrease the plant defense system against insect pests, thus making them vulnerable to damage (Dhaliwal et al., 2010). Moreover, elevated temperature and CO₂ levels can affect the herbivore-induced plant volatile (HIPV) and the olfactory perception of volatiles, which can affect the host-finding ability of natural enemies and the efficiency of biological control (Bruce and Pickett, 2011; Thomson et al., 2010; Gouinguéné and Turlings, 2002). Several studies have also shown poor synchronization between parasitoids and their hosts (Chen et al., 2007; Grabenweger et al., 2007). Phenological shifts within and in between trophic levels are changing biotic interactions. These asynchronies contribute to restructuring of insect communities (Damien and Tougeron, 2019). So, climate change has far-reaching consequences on the interactions between plants, herbivores, and natural enemies.

Efficacy of behavioural method: Pheromone communication

It is likely that higher temperatures and changing atmospheric CO₂ and O₃ levels will affect the entire process of pheromonal communication, from production to behavioral response. Insects that rely on long-range chemical signals for communication are expected to be most affected, as these signals may be exposed to oxidative gases during dispersal (Boullis et al., 2016). Unsaturated terpenes, which are constituents of sexual,

alarm, or aggregation pheromones in several insects, such as aphids (Boullis and Verheggen, 2016; Francis et al., 2005), bark beetles (Taft et al., 2015), and fruit flies (Sarles et al., 2015), may be altered by ozone. Moreover, raised temperatures are expected to impact pheromone biosynthesis both qualitatively and quantitatively, as insect's enzymatic activities are influenced by its changing body temperature with the environment (Neven, 2000). For example, the ratio of compounds in the sex pheromone may change with temperature in the potato tuber moth *Phthorimaea operculella* (Ono, 1993). Additionally, warmer rearing conditions of the larvae of *Philanthus triangulum* increased the production of pheromonal secretions in adult males and the percentage of compounds with high molecular weight in pheromones (Roeser-Mueller et al., 2010). Temperature changes may also alter the shape of scent plumes and affect the efficiency of insects reaching their target in pheromones dispersed over long distances (McFrederick et al., 2009). Furthermore, elevated CO₂ levels can alter the ability of aphids to produce and/or respond to the alarm pheromone, which impacts their defensive behaviors (Sun et al., 2010). Several reports demonstrate that climate change by increases in temperature and atmospheric gas concentrations can interfere with insect pheromone communication in insects (Renou and Anton, 2020). As climate change may also modify the behavioral reaction of insects to pheromones and allelochemicals, all semiochemical-based insect management strategies may be impacted. Evidence suggest that climate change affects pheromone molecule stability, thus reducing its biological efficacy under field, so climate change could be a general problem for chemical communication in insect species (El-Sayed et al., 2021).

Effect on insect indirectly through host plants

The effect of climate change on insects will be indirect too due to the change in vegetation affected by climate change. Vegetation not only responds to climate change but also create a distinct microclimate pattern (Ramamurthy, 2009). Insect's life cycle and development are intrinsically linked to their host plant phenology, which is primarily governed by temperature conditions in the surrounding environment (Bale et al., 2002; Szujeci, 1998). So, alterations in temperature, CO₂ and humidity levels can impact insects by changing the host plant's physiology and metabolism (Netherer and Schopf, 2010; Moore and Allard, 2008; Stevens et al., 2004). Furthermore, an increase in average temperature can affect plants and phytophagous insects

differently, potentially disrupting the synchronization of critical processes at different trophic levels within an ecosystem (Visser and Holleman, 2001). Increased CO₂ levels are expected to affect plant physiology by enhancing photosynthetic activity, leading to improved plant growth. While C4 plants are less sensitive to increased CO₂ and less likely to be impacted by changes in insect feeding behavior, C3 plants are more likely to be positively affected by elevated CO₂ levels and negatively influenced by insect feeding (Lincoln et al., 1984). Plants' carbon: nitrogen ratio changes with increased CO₂ levels since they tend to store more sugars and starches in their leaves (Cotrufo et al., 1998) which may further affect insect feeding behavior and metabolism. Changes in the frequency, duration, and intensity of rainfall are predicted under climate change (Chen et al., 2019). This rainfall change will affect the soil moisture, which is important for many soil dwelling insects (Ramamurthy, 2009).

CONCLUSIONS

Greenhouse gases emission are considered major cause of climate change and agriculture sector responsible for approximately 21% of global greenhouse gas emissions. Insects, being highly dependent on the thermal conditions of their environment, are highly vulnerable to climate change. Predicting the impacts of climate change on insect pests is challenging due to the complex interactions of increasing atmospheric CO₂ concentration, changing climatic regimes, and altered intensity/ frequency of extreme weather events. Increasing of temperatures, atmospheric CO₂ levels, and altered precipitation patterns impacting insect directly and indirectly. While insects are adaptable organisms that respond differently to various impacts of climate change, the rising temperature can lead to a range expansion, increased overwintering survival, and changes in their interactions with host plants and natural predators. The rising CO₂ level can affect the consumption rates, growth rates, fecundity, and population densities of insect pests. Altered precipitation patterns can favor the incidence of droughts and floods, which can affect insect survival and diapause. Some species are better adapted to changing climates and may proliferate and become invasive while a large number of species are unable to adjust their complex life event to changing dimensions of climate. Even though impacts on insect pests, induced by climate change are variable and subject to various interacting factors, it is expected to cause an increase in the latitudinal and altitudinal distribution range of insect species. The

distribution and range of insect species are shifting, with many pests spreading beyond their traditional boundaries. Further, it may also impact phenological synchronization and patterns of species interactions, and species complex of a region. Additionally, the impact of climate change on insect ecology is significant and multifaceted, affecting insect communication, behavior, and interactions with plants and natural enemies. Changes in plant phenology and defensive traits, coupled with altered insect communication systems, pose further challenges to plant-herbivore-natural enemy interactions, potentially affecting the efficiency of biological control. Also, climate change together with continuously increasing trade can be favourable for invasive phytophagous insect species. Understanding these complex interactions is crucial for developing effective strategies to correctly predict the future trend of insect pest and successfully managing them.

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(Manuscript Received: November, 2022; Revised: May, 2023;

Accepted: May, 2023; online Published: May, 2023)

Online First in www.entosocindia.org and indiantentomology.org Ref. No. e23899