



Abiotic Factors as Game Changer in Sex Ratio Distortion of Insects

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Sex ratios in insect populations are critical in shaping their reproductive dynamics, genetic diversity, and ecological interactions. While genetic factors often determine sex, abiotic factors have emerged as important influencers of sex ratios in insects. The influence of abiotic factors on sex ratios in insects is of scientific interest and holds practical implications for insect conservation and management. As environmental conditions change due to global warming, understanding how sex ratios respond to these changes can aid in predicting population dynamics and designing effective conservation strategies for biocontrol agents as well as the management of insect pests. Abiotic stressors, including fluctuations in temperature, humidity variations, altitude & latitude, nutrition and chemical exposure have been shown to disrupt the precise balance of hormonal and genetic cues governing sex determination in insects. Insects being ectothermic, body temperature depends on the surrounding environmental conditions and are highly vulnerable to the change in climate. This

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review explores the intricate relationship between abiotic stress and sex determination mechanisms in insects, highlighting recent advances in our understanding of how stress-induced alterations especially environment in hormone signaling, gene expression, and epigenetic modifications can lead to skewed sex ratios and developmental anomalies. Regardless of the advances in this area, notable research gaps are still present. Future studies on the multiple abiotic factors and their synergistic effects will give a more detailed study of insect populations, and their ecosystems. This comprehensive review delves into the multifaceted interactions between abiotic factors and sex differentiation in insects. In conclusion, the abiotic factors especially temperature are indeed game changers in the insect sex ratio dynamics.

Keywords: Abiotic factors; sex ratio; epigenetics; juvenile hormone; metamorphosis.

1. INTRODUCTION

The sex ratio in insects has long been a subject of fascination and research due to its implications on population dynamics and evolutionary biology. While the underlying mechanisms remain complex and multifaceted, it is well established that abiotic factors especially temperature play a crucial role in shaping the sex ratio of these insects [1-4]. As explained that natural selection effects on the sex ratio predict an evolutionary equilibrium in the population as parental reproductive resources are portioned equally

between males and females causing a 1:1 sex ratio [5].

A most important adaptation in insects *i.e.* diapause is a state which allows the insect to survive adverse environmental conditions where the growth, development, and reproduction are temporarily paused in insects. The diapause that occurs at a certain developmental stage in organisms regardless of environmental conditions is obligatory while facultative diapause which is the more common type is mainly intended on environmental signals [6].

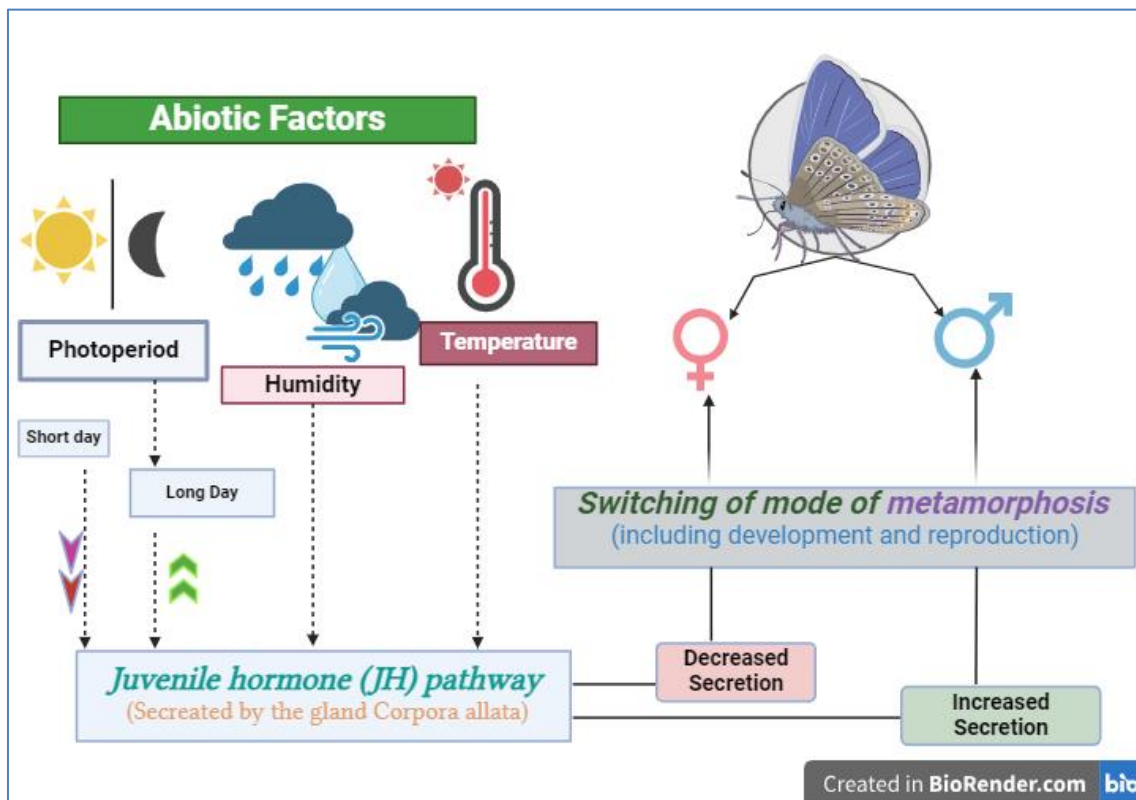


Fig. 1. Abiotic factors causing sex ratio distortion in insects (61, Created with BioRender.com)

Sánchez [7] envisaged that sex determination in organisms, which guides the developmental pathway is influenced by zygotic, maternal, and environmental situations. However, abiotic factors, such as temperature, photoperiod, and nutrition, can also modulate the expression of sex-determining genes, leading to shifts in sex ratios within populations [8]. Understanding the mechanisms influenced by abiotic factors is crucial for comprehending the plasticity of sex determination in insects. It was pointed out about the area of discord *i.e.* allocation of sex in bees, eusocial ants, and wasps. Haplodiploidy in them means that workers and queen have diversity in genetic relatedness to males and females formed in their colony, thus leading to a change in the optimal sex ratio [9]. Fig. 1 highlights the different abiotic factors affecting the sex ratio of insects.

The objective behind studying the ideal sex ratio in insects is that, it is an important factor for the stability of its population, ecological balance and genetic diversity. By investigating the complicated mechanism behind sex determination, it can be better predicted and its impact can be mitigated by the scientists. Thus, the pest and the vectors for disease control can be improved. We can effectively support their ecological roles, develop sustainable solutions and promote biodiversity.

By analysing the gaps regarding abiotic factors influencing the sex ratio of insects is necessary for the strategies regarding pest and vector control, agricultural productivity maintenance, supporting conservation initiatives and maintaining ecological equilibrium. More research studies in his field will be beneficial for the environment and human health too. In this review, we delve into the various abiotic factors that have been documented to influence the sex ratio of insects, highlighting their significance in driving evolutionary outcomes and ecological dynamics. Different abiotic factors affecting the sex ratio of insects have been discussed below.

2. PHOTOPERIOD

There is evidence of photoperiodism altering the sex ratio in rotifers, lizards, turtles, gastropod mollusks, polychaete and oligochaete annelids, fish, echinoderms, frogs, and mammals [10]. Photoperiod, or the duration of day and night cycles, has been identified as a critical cue affecting sex determination in *Drosophila melanogaster* [11]. The ability of insects to sense changes in day length and adjust their

reproductive strategies accordingly has significant implications for population dynamics and seasonal adaptations. The onset of important events in insects such as reproductive diapause, and sexual differentiation being regulated seasonally depends on photoperiod. These events are complex process that includes photoreception, day and night length calculation, covert effects incorporation and preservation of photoperiods through a counter mechanism, thus, endocrine effectors ultimately regulate the responses accordingly [12]. A study shows that in univoltine species, diapause is an obligate part of their life, while in multivoltine species it seems to be facultative and needs an environmental trigger like photoperiod etc [13]. In response to photoperiodism, the insect shuts down its development and reproduction [10]. The evolution of many traits involves components of different mechanisms, such as plastic responses to photoperiod in relation to climate change [14]. Specific photoreceptors perceive the photoperiodic information which is transmitted to a photoperiodic clock, that measures the photophase or scotophase lengths to ascertain the specified photoperiod a long day (LD) or a short day (SD) [15]. This information about LD or SD is further shuttled to the regulatory system that persuades responses like diapause/decrease growth rate or non-diapause/swift growth rate and the evidence suggest that the photoperiodic clock is regulated by the circadian clock [16]. A study confirmed that photoperiod and temperature are the two factors involved in regulating the nymphal development of *M. siamensis* [17]. It was suggested that the photoperiod regulates Ms'myo, and the JH signaling pathway. Short days activate juvenile hormone (JH) and down-regulate myoglianin (Ms'myo), a member of the TGF β family that induces adult metamorphosis. However, in contrast to this, long days upregulate Ms'myo expression during the fifth to sixth instar to initiate adult metamorphosis. Suppression of Ms'myo expression leads to upregulation of juvenile hormone O-methyl transferase (Ms'jhamt), thus, increases molts and nymphal period prolongs even under long-day conditions [17].

3. HUMIDITY AND PRECIPITATION

Humidity and precipitation levels can significantly influence the survival and reproductive success of Lepidopteran insects [18]. These abiotic factors can affect larval development, adult behaviour, and mating success, thus leading to

shifts in sex ratios within populations. One interesting example of a seasonal polyphenism can be seen in tenebrionid beetle, *Cryptoglossa verucossa*, that exhibits different colour types ranging from jet black to light blue because of the different humidity conditions of the prevailing environment. The different color phases that arise from the wax secretions are helpful in the regulation of water balance and body temperature being faced in desert conditions [19]. Humidity is an important factor in regulating the whitefly populations. High temperature and increased humidity build up the whitefly population [20].

4. ALTITUDE AND LATITUDE

Elevation and geographical location are associated with changes in environmental conditions, which can impact the distribution and abundance of insect species [21]. Studies have demonstrated that sex ratios can vary at different altitudes and latitudes, shedding light on the adaptive strategies employed by these insects to cope with changing environmental gradients.

5. NUTRITIONAL CONDITION

Nutritional condition during development have been shown to impact sex ratios in various insect species [22]. Understanding the nutritional basis of sex determination sheds light on the adaptability of insects to variable food resources and the implications for their population ecology. It was studied by Verma et al. [23] that the change in the host of *Kerria lacca* lead to the change in its sex ratio. Higher number of males was observed under adverse conditions and poor nutrition that resulted in a distorted sex ratio due to nutritional condition. Variation in nutrition may cause mortality differences among different sexes causing biased sex ratios. Nutritional stress effects on the sex ratio of spruce budworm (Lepidoptera: Tortricidae) were studied by Quezada-García et al [24]. Nutritional stress effects on pupae and adults sex ratio showed a biased sex ratio which favoured males and fewer females. A study on spruce budworm, *Choristoneura fumiferana* highlighted that parental nutrition has direct and indirect potential affects which can be observed in next-generation offsprings of the insect [25]. Parental feeding pattern affect the size and quality of the following population. It was further studied by Mopper and Whitham [26] that simultaneous abiotic stress such as low precipitation on insect host plant trees while the insect is ovipositing or feeding on

the host reduces its performance. Contrasting to this, sustained abiotic stress like prolonged drought conditions or poor conditions of soil deficient in essential nutrients benefits insect performance.

6. TEMPERATURE

Due to the small stature and ectothermic metabolism of insects, they are particularly susceptible to high temperatures. Exposure to such environments constitutes a daily threat to their survival. Temperature plays a pivotal role in sex differentiation in many insect species, and it operates through a phenomenon known as Temperature-Dependent Sex Determination (TSD), a biological phenomenon observed in many reptiles, some fish, and certain insects, including some lepidopteran species [27]. TSD has been reported in a number of taxa including vertebrates and invertebrates [28]. In TSD, the sex of the offspring is determined by the temperature experienced during a critical period of development, usually during the early stages of embryonic development. Heat tolerance is generally estimated by survival-related metrics which include; critical thermal maximum (that causes temperature failure), median lethal temperature (resulting in 50% mortality of exposed individuals) and upper lethal temperature (causing mortality in a specified fraction of individuals exposed) [29]. The sex determination mechanism can be either based on the duration of exposure to a specific temperature or the temperature experienced at a specific developmental threshold. This is in contrast to the more common XX/XY sex determination found in mammals and many other animals. The first report suggesting that temperature could influence the sex ratio was published from observations in a lizard from West Africa, *Agama* [30]. In diamondback moth (*Plutella xylostella*: Lepidoptera), TSD can play a crucial role in controlling the developmental life period within a population [31]. The exact mechanism of TSD can vary among species, but generally, it involves the sensitivity of developing embryos to temperature cues, which subsequently influences the sexual differentiation process.

Temperature being the most important abiotic factor regulating the development and controlling the reproduction of arthropods, its impact and role in sex allocation of haplodiploid arthropods is still unexplored. Temperature-dependent sex determination (TSD), where incubation

temperature during a critical developmental window determines an individual's sex, is a well-documented example. Many reptiles, such as turtles, as well as certain insect species, including some butterflies and ants, exhibit TSD [32]. Understanding the mechanisms underlying TSD and its ecological implications is crucial for predicting sex ratio responses to climate change [33]. High-temperature exposure to *Ephestia cautella* and *Plodia interpunctella* reduces the fecundity of respective insects [34]. Likewise, the rearing of *D. melanogaster* at high temperature leads to cytoplasmic factor elimination, thus altering its sex ratio [35,36]. It is important to note that the specific temperature thresholds and the critical periods of sensitivity for TSD can vary significantly between species [29]. The different conditions are; mixing of generations; temporary changes in life history expectations of both the sexes; and parental ability to change the sex in response to different environmental changes [35]. As studied earlier it clearly demonstrated that the temperature and RH had profound effects on incubation, larval and pupal periods as well as on adult emergence and sex ratio in the experimental insects [37].

It is obvious from the present assessment that the lower temperatures (25°-28° C) and moderate RH (60-75%) are appropriate for the immature development and adult emergence in *B. mori* whereas higher temperatures (28°-32°C) elevated RH (80-95%) shortened immature developmental periods, leading to poor performance of the silkworm lines. These findings correlate to the climate change issue, which has been recognized as a major threat to the survival of species and the integrity of ecosystems worldwide [37].

7. DISTORTED SEX RATIO DUE TO TEMPERATURE/ HEAT STRESS

Distorted sex ratio changes result in sexual aggression, parental cooperation breakdown and mate shortage [38]. It also limits sexual selection, changes effective population size and increases the risk of extinction [39]. The biased sex ratio reduces the ability of a species to change its habitat due to the changed climate if it is male biased but it enhances in case of female biasedness [40].

Importantly, male- and female-biased sex ratios are expected to have different consequences, with male bias expected to be more detrimental to population growth and viability, as both are

often constrained by female fecundity [29]. There are three main mechanisms through which high temperature can distort sex ratios. One mechanism is sex-biased heat tolerance, which refers to sex differences' ability to survive high-temperature exposure/ treatment. A second mechanism is temperature-dependent sex determination (TSD), meaning cases in which sex is not determined genetically, and is instead controlled by the environmental temperature experienced during development. A third mechanism is temperature-induced sex reversal, which refers to cases in which sex is initially determined genetically, but is then altered by environmental temperature [29], thus changing the sex of the insect by either causing masculinization effect or feminization effect in insects.

Distorted sex ratios can increase mate shortages, sexual aggression, and breakdown in parental cooperation [38]. Allocation of sex is a foremost fitness-related decision that changes concomitantly with the change in environmental factors, as confirmed and predicted theoretically and conducted experiments by West [41].

Earlier reports support that a single hot day caused detrimental effects on reproduction, primarily owing to maternal effects on the hatching of eggs, thereby influencing the diamondback moth (Lepidoptera) population dynamics [42]. When *kerria lacca* was cultured on different hosts for different seasons, then the change in sex ratio was observed suggesting that temperature and even nutrition play an important role in changing the sex of an insect [23].

When *Drosophila virilis* was heat stressed than female-biased sex ratio was observed [43]. Thermal stress effects as studied by Reshma et al., [35] showed that when *Spodoptera frugiperda* larvae were heat stressed then this resulted in reduced maturation success, prolonged developmental duration and biased sex ratio with a greater number of females. As reported earlier in insect parasitoids that at high temperature a behavioural change is observed in the sex allocation, which leads to more number of males to avoid competition and at low temperature, egg fertilization was prevented due to the physiological constraints, which again lead to increase in males' proportion, which were previously intended to become females. Thus, temperature harmonizes physiological

constraints in fertilization of eggs and allocation of sex in parasitoids [44].

When *Campoletis chlorideae* Uchida was heat stressed, the progeny sex ratio resulted in increase in number of females *i.e.*, female biased when treated within a range of 17-27°C [45]. Similarly, *Lymantria dispar* pupae when exposed to abnormal temperature resulted in adults that have the characteristics of both males and females [46]. When the eggs of *Solenobia triquetrella* was exposed to 34°C for 12 hr. or 2-3 days for 4 °C and 6 °C resulted in masculinized females, thus distorting the sex ratio [47]. It was concluded that some factors mainly elevated temperature influences the chromosome behaviour during meiosis or early cleavage stages of the egg nucleus, but the precise mechanisms of sex determination depends on the genetic system of different groups [9].

8. SEX-SPECIFIC RESPONSES UPON TEMPERATURE CHANGE

Sexual dimorphism *i.e.*, males and females of same species with differential biological processes have different gene expressions in both the sexes [48]. Different sex genes have different types of gene expression in response to the changed temperature. Sex-biased gene expression pattern is extremely species-specific across butterfly species as in *Eurema hecabe*, indicating that response of sex-biased gene expression to climate change is challenging in butterflies [8]. A study suggests that selection promotes some genes resulting in the temporary overproduction of one over the other sex, under changed environmental conditions. It has been reported that sex-biased genes dependent on temperature are more in females as compared to males, it also includes genes which are involved in different vital biological functions, focussing on the potential ecological effects of increased temperatures [8]. So, it was concluded that different tissues of contrasting sexes of *E. hecabe* showed discrete response across different temperature range including differential expression of key genes for hormone synthesis as well as noncoding micro-RNAs [8]. When *Plutella xylostella* was exposed to higher temperature, results showed higher expression of Hsp 90 & Hsc 70 genes in females as compared to males [49]. This coincides with results reported earlier that female insects are less affected to high temperature than male insect of *Bradysia odoriphaga* [50].

9. EPIGENETIC REGULATION OF SEX CHROMOSOMES

Russo et al defined it as “the study of meiotically/ mitotically heritable changes in gene function that cannot be explained by DNA sequence changes” [51]. Epigenetic regulatory phenomenon examples include temperature dependent vernalization in plants, mating type silencing in yeast, gametic imprinting, and X- chromosome inactivation in mammals [52]. Major epigenetic mechanisms for gene expression regulation include modification of histones, DNA methylation, modification of histone variants and the presence of ncRNAs (non-coding RNAs) [52]. However, not resembling the other types of epigenetic information, DNA methylation is not present in many insect genomes. The relationship between environmental factors, temperature, and epigenetic modifications is complex. An insect’s ability to develop its phenotype in accordance with its environment depend on the epigenetic information [53]. These environmental changes can be intercellular and extracellular bringing about the heritable changes. The transmission of epigenetic information within individuals is through mitotic cell division, and through meiotic cell division to the offspring [54]. These epigenetic transmissions could be intragenerational and intergenerational inheritance. Intragenerational epigenetic inheritance is mainly concerned with development process and discusses the mysteries surrounding the development of a single set of genetic instructions from an egg into a multicellular creature consisting of several tissues [55]. Conversely, intergenerational epigenetic inheritance discusses how these epigenetic information gets transferred to the offspring [56].

It was proposed by Berger et al [57] that, three types of signals operate sequentially for the stable establishment of heritable epigenetic state. The signal (for e.g. temperature signal or differentiation signal) which the cell receives from its environment is called epigenators. Responding to this epigenators signal, the epigenetic initiator (the second signal) is cell’s respond signal that forms a localized chromatin context at an exact site by identifying specific sequence. Epigenetic maintainer is the third signal that sustains and perpetuates the change in chromatin that is transferred from parent to offspring.

Recent research has shed light on the crucial role of epigenetic mechanisms in the regulation

of sex determination genes. Sex chromosomes are subject to unique epigenetic modifications, leading to dosage compensation and sex-specific gene expression. Gorelick [58] hypothesized that dioecy and sex chromosomes originated in ancestral diploid hermaphrodites as a pair of autosomes in which one chromosome had more methyl groups near to a sex-controlling region than did its homologue. Methylation would suppress transcription, including loci for gamete production hence transforming hermaphrodites into males or females. Differential methylation would also suppress recombination, increasing the speed of Muller's ratchet, the same hypothesis was also postulated by Jablonka [58]. One of the predictions of this point of view was that species with ESD require homomorphic sex chromosomes and those small environmental changes can alter the methylation patterns of sex-related loci, therefore determining the sex of individuals [58,59].

Through behavioural avoidance, migration, diapause, or substantially altered physiological conditions, insects escape temperature extremes [18]. These epigenetic modifications are reversible; thus, it represents an important role in balancing between reversibility and maintenance [60].

10. JUVENILE HORMONE AND ITS ROLE IN INSECT SEX DIFFERENTIATION

Amidst the captivating realm of insects, development, transformation, and reproduction are all orchestrated in a way akin to a complicated symphony conducted by an ensemble of hormones. One of the important hormones in this complex hormonal orchestra, stands out as a central figure is the juvenile hormone (JH). Juvenile hormone, earlier known as "inhibitory hormone" was first reported in 1936 in *Rhondius prolixus* by Sir V. B. Wigglesworth. Juvenile hormone is the methyl ester of epoxy farnesoic acid and has a unique terpenoid structure. JH is a class of insect hormones that holds the key to many of the remarkable transformations and adaptations observed in the insect kingdom. This hormone is synthesized by the gland corpora allata. These are categorized into eight types such as; JH 0, JH I, JH II, JH III, 4-methyl JH I (Iso- JH 0), JHB III, JHSB III, and MF. Its regulation and biosynthesis are affected by photoperiods, temperatures, diet and plant compounds. Analogue of juvenile hormone disrupting JH normal regulation is classified as insect-growth regulators (IGRs).

In the insect's larval stages, JH is present but prior to transition from pupa to adult, it gets eliminated. Compared to other stages of life cycle, the highest concentration of hormone is present in adult moths. Particularly, the adult male than that of adult female has its highest concentration. In both the sexes of an insect, *dsx* gene is transcribed which gets spliced differentially according to male or female specific mRNA. Both of these transcripts have DNA binding domain which contains a zinc finger that regulates tissue sexual differentiation during development of an insect. It was further reported that there exists a functional link between the signalling of JH and expression of *dsx* gene [61].

11. FUTURE PROSPECTS

Sex ratio in insects can be manipulated through different environmental factors as they are ectothermic so it can be used in managing the population dynamics of insects. Thermal stress strategies can be utilized for pest management, likewise, genetically engineered fruit flies produce sterile male populations when treated at high temperature. Can we anticipate whether species will adjust its sex ratio due to warming temperature? The goal is to either have balanced sex ratio to have maximum effective population size or to have female biased sex ratio to increase the population growth.

12. CONCLUSION

Distortion of sex ratio is an understudied area of research, yet it is a widespread issue taxonomically. A principal factor that delimits the reproduction and survival of insects is temperature. High temperature exposure (below lethal high temperature) can cause thermal injury to the insects leading to reduced fitness and survival, which can be observed during the developmental period of the life cycle. Reproductive parameters are hypersensitive to a higher temperature than survivability and is a visionary to climate change effects on the population. Both basal tolerance and plastic responses contribute to the ability of ectotherms to counter heat stress.

Many taxonomic groups like dipterans, hemipterans, lepidopterans, reptiles have higher female and higher male tolerance to different environmental conditions especially temperature, thus sex biased tolerance seems to be highly labile. Much attention is required for carrying out additional research on different factors causing the sex ratio distortion in insects.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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