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Four seasons: Diversity of seasonal adaptations and ecological mechanisms controlling seasonal development in true bugs (Heteroptera) in the temperate climate.

Seasonal adaptations of terrestrial, semiaquatic and aquatic true bugs (Heteroptera) from the Temperate Zone are thoroughly reviewed according to the four seasons of the year cycle when these adaptations are manifested.

In autumn, the waist majority of heteropterans enter facultative or obligatory winter diapause. Out of 163 species from 27 families included into analysis, almost 70% of species are known to overwinter as adults, 19% – as eggs, and only 4.3% – as nymphs. A small number of species can successfully overwinter in different life cycle stages (3.7%) or have long life cycles and, thus, overwinter more than once (3.1%). Induction of the winter diapause in many true bugs is controlled by the photoperiodic response of the long-day type: individuals are physiologically active under long-day conditions, but enter diapause under short-day ones. In the case of embryo diapause, the parents are usually sensitive to day-length in their nymphal or adult stage and, thus, can produce diapause or non-diapause eggs depending on the environmental signals they receive. Species with nymphal diapause are mostly sensitive to day-length in the preceding nymphal instars. In the case of adult diapause, sensitivity to day-length may be associated with different nymphal instars and/or early adult stage.

Environmental factors other than day-length can take part in induction of diapause too. Thus, temperature can strongly affect incidence of diapause induction and/or the critical photoperiod of the response, though we are still lacking solid evidence that temperature can be the principal factor or cue in the induction of diapause in Heteroptera species. Diapause response can also be strongly modified by food (typically the effect of early season vs. late season food). Combined effects of day-length, temperature, food, and perhaps other factors ensure precise timing of diapause induction.

Seasonal polyphenism (also known as ecological, or environmental, polymorphism) represents a special case of insect polymorphism when incidence of distinct forms (morphs) is controlled by environmental conditions. The two categories of seasonal polyphenism that are most important and widely spread among Heteroptera species are wing (or alary) and

body colour polyphenism. In many species of aquatic and semi-aquatic true bugs, adults of the reproductive (i.e. summer) generation(s) tend to be short-winged (what allows allocating more resources for reproduction), whereas those of the diapause (i.e. overwintering) generation tend to be long-winged (what can greatly enhance migration to better protected overwintering sites). The control of wing morph determination is usually very complex and can involve responses to day-length, temperature, food conditions, population density, state of the water body, etc. A strong genetic component is often involved too.

Seasonal colour polyphenism may be reversible or irreversible and it is often associated with diapause. In the case of reversible changes, individuals of the overwintering generation change colour (usually from bright or green to more protective brown) in autumn but restore their usual colour in spring (e.g., in the pentatomids *Nezara viridula* and *Plautia crossota stali*; all references are shown in the review). In the case of irreversible changes, the colour cannot change after reaching the adult stage, and reproductive and overwintering generations simply differ in coloration. For seasonal morphological polyphenism, morphs differ in morphological traits (e.g., external structures, pubescence or thickness of cuticle).

In many heteropteran species, adults of both sexes overwinter prior to reproduction in a diapause state with undeveloped reproductive structures. In some species, however, males may have mature sperm and copulation not only takes place during the winter, but also may increases chances of survival in females (e.g., in the pentatomid *Menida scotti*). In a number of flower bugs (Anthocoridae), only females normally survive winter. Adults of the late-autumn generation of *Orius* spp. copulate in autumn and males usually die prior or during the winter, whereas females survive, store sperm and produce eggs in the spring.

Freeze avoidance seems to be the principal cold tolerance strategy of heteropterans for survival of subzero winter temperatures. Removal of ice nucleators that initiate ice formation, synthesis of antifreeze proteins, and accumulation of sugars and polyols allows bugs to keep their body fluids liquid at low temperature. Supercooling point may change during the seasons being typically lower in the winter (e.g., in the acanthosomatid *Elasmostethus interstinctus* and the pentatomid *Graphosoma lineatum*).

Termination of the winter diapause can happen spontaneously or in response to changes of environmental conditions (e.g., day-length and/or temperature). Low temperature exposure does not seem to be required for diapause termination, especially in the species with facultative diapause. Under natural conditions, the intensity of diapause usually decreases as the winter months pass and in the late winter most species are in quiescence rather than deep true diapause (e.g., in the fire bug *Pyrrhocoris apterus*). In some species, however, diapause seems to be maintained much longer (until the spring) by short day (e.g., in the belostomatid *Lethocerus deyrollei* and the coreid *Anasa tristis*).

In spring, resumption of normal development and feeding and start of reproduction in most species seem to be chiefly restricted by temperature conditions and availability of food. After winter, some species can also change body colour back to non-overwintering state (e.g., the pentatomid *Nezara viridula*) and/or have migratory flights from overwintering sites to breeding ones (e.g. many gerrids).

Summer adaptations of true bugs are also diverse. Duration of nymphal period is mostly controlled by temperature and food conditions but day-length has been shown to influence it too. Thus, shortening photoperiod is a precursor of approaching autumnal deterioration of environmental conditions and as such is used by some species to accelerate growth of nymphs and draw closer the moulting to the adult stage (e.g., in the pentatomid *Palomena prasina* and the fire bug *Pyrrhocoris apterus*). Day-length and temperature may also affect coloration of nymphs in some species, presumably participating in thermoregulation.

A few species of true bugs are known to have summer diapause, an adaptation that allows survival of the hot and, thus, unfavorable periods in mid-summer, better synchronization of the seasonal cycle with resources and/or maintenance of the univoltinism (e.g. in the scutellerid *Eurygaster integriceps* and the pentatomid *Picromerus bidens*).

In general, the thermophilic nature and high temperature requirements of true bugs influence their geographic distribution and limit number of annual generations.

In the preliminary eco-phylogenetic analysis we tried to find out whether particular families and infraorders of Heteroptera have typical overwintering (diapause) stage and wing morphs. To do so, the data on the known overwintering stage(s) and wing morphs were superimposed on the dendrograms of the phylogeny of Heteroptera.

In many families of true bugs, it is known that different member species overwinter in different stages. Thus, in nine out of 38 families included into analysis there are examples each representing one of all three (i.e. egg, nymphal, and adult) overwintering stages (e.g., Veliidae, Corixidae, Aphelocheiridae, Reduviidae, Tingidae, and Pentatomidae). However, within the four better studied infraorders (i.e. Gerromorpha, Nepomorpha, Cimicomorpha, and Pentatomomorpha), the adult stage is the only known overwintering stage for 14 out of 38 analyzed families (e.g., Hebridae, Macroveliidae, Hydrometridae, Belostomatidae, Anthocoridae, Coreidae, Acanthosomatidae, and Cydnidae) and this stage may be considered typical (or dominant) overwintering stage for a few other families (e.g., Gerridae, Naucoridae, Tingidae, and Pentatomidae). Overwintering in the egg stage is typical for Mesoveliidae, Veliidae, Notonectidae, Saldidae, Reduviidae, and Miridae. The nymphal stage may perhaps be considered typical overwintering stage only in Reduviidae and Cimicidae, even though there are individual species in other families that overwinter in this stage too (e.g., in Veliidae, Ochteridae, Aphelocheiridae, Saldidae, Plataspidae, and Aradidae).

The distribution of different wing morphs shows a very complex pattern in Heteroptera. A full-winged (macropterous) morph is known in all 42 families included into analysis, except Cimicidae (and also Polyctenidae, which was not included). Complete or partial and constant or temporal wing reduction (as in brachypterous, micropterous, and apterous morphs) is known in 31 families included into analysis. It is believed to be mostly associated with the life style pattern of a species and more frequently observed in predators, parasites and/or species living under tree bark, on the soil surface or close to water (e.g. in Aenictopecheidae, Veliidae, Aphelocheiridae, Saldidae, Reduviidae, Cimicidae, Pyrrhocoridae, and Aradidae). The wing morphs are perhaps more diversely represented in Enicocephalomorpha, Dipsocoromorpha, and Gerromorpha than in Nepomorpha and Pentatomomorpha.

It is suggested that secondary wing reduction (i.e. wing polyphenism/polymorphism) as well as different diapause patterns evolved independently and many times in different groups of Heteroptera.

In general, diverse seasonal adaptations such as facultative and obligate diapauses, winter and summer dormancies, different ecological and physiological strategies of cold survival, behavioral responses, seasonal polyphenism, migration, growth rate control strategies, etc. are widely used by Heteroptera species to survive and successfully utilize resources under conditions of pronounced seasonality typical for the Temperate Zone. This makes seasonal cycles and phenological patterns of true bug species very diverse and different from each other even when the species are phylogenetically close or occupy similar habitats.