

Diapause in Insects

Many species of insects have evolved a strategy called diapause. Diapause is a suspension of development that can occur at the embryonic, larval, pupal, or adult stage, depending on the species. In some species, diapause is facultative and occurs only when induced by environmental conditions; in other species the diapause period has become an obligatory part of the life cycle. The latter is often seen in temperate-zone insects, where diapause is induced by changes in the photoperiod (the relative lengths of day and night). The day length when 50% of the population has entered diapause is called the critical day length, and it is usually quite sudden. Insects entering diapause when the day length falls below this threshold are called long day insects. Those insects that develop normally when there are only a few hours of sunlight and that enter diapause when exposed to longer days are called short-day insects. The critical day length is a genetically determined property (Danilevskii 1965; Tauber et al. 1986).

Diapause is not a physiological response brought about by harsh conditions. Rather, it is brought about by token stimuli that presage a change in the environment. Diapause begins before the actual severe conditions arise. Diapause is especially important in temperate zone insects that overwinter. Embryos of the silkworm moth *Bombyx mori* overwinter as embryos, entering diapause just before segmentation. The gypsy moth *Lymantria dispar* initiates its diapause as a fully formed larva, ready to hatch as soon as diapause ends. Other insects experience diapause as eggs, pupae, or even as adults.

In the silkworm *Bombyx*, embryonic diapause appears to be regulated by diapause hormone, a 24-amino acid peptide that is produced in the subesophageal ganglion (Fukuda 1952, Hasegawa 1952). This hormone acts on the maturing oocytes in the pupal stage and causes development to stop once the embryo has reached about 12,000 cells (Kitazawa et al. 1963). The regulation of the gene encoding the diapause protein has been seen to be induced by temperature (Xu et al. 1995).

While diapause in the embryonic stage appears to be regulated (at least in some species) by a diapause hormone, larval diapause appears to be controlled by the inhibition of PTTH production. This prevents the larvae from molting and entering pupation. In many butterflies, this inhibition of PTTH is due to a continued elevated titre of juvenile hormone. Similarly, the lack of PTTH and ecdysone secretion once pupation has occurred will cause diapause during this part of development. Diapausing pupae can be reactivated by adding back 20-hydroxyecdysone. However, under normal conditions, the brain of diapausing pupae (such as those of the moth *Hyalophora*) is activated by the exposure to cold weather for a particular duration. Moth pupae kept in warm conditions will remain in diapause until they die (see Nijhout 1994). The mechanism by which these temperature and day length changes regulate hormone production remains to be elucidated.

The ability to time one's development to season, temperature, or even tides is a critical property of many organisms. In some species, the timing of development has to take several ecological variables into account simultaneously. One sees such an example in the baroque life cycle of a *Clunio marinus*, a small fly that inhabits tidal waters along the coast of western Europe. Females of this species live only 2-3 hours as adults, and they must mate and lay their eggs within this short time. To make matters even more precarious, egg laying is confined to red algae mats that are exposed only during the lowest ebbing of the spring tide. Such low tides occur on four successive days shortly after the new and full moons (i.e., at about 15-day intervals). Therefore, the life cycle of these insects must be coordinated with the tidal rhythms as well as the daily rhythms such that the insects emerge from their pupal cases during the few days of the spring tide and at the correct

hour for its ebb (Beck 1980; Neumann and Spindler 1991). This non-biting midge has synchronized its life cycle to the lunar-based tides. Adults live but a few hours and reproduce only when the tides are so low as to expose certain algae. These tides recur around the new moon and full moon, and *Clunio* adult emerge for a few days around the spring tides (Kaiser et al 2011). Moreover, the midges emerge for only a short time at the beginning of the low tide. Thus, their life cycle is synchronized by both a lunar clock and a solar clock. The emergence rhythms continue for months even if the larvae are taken into the laboratory.

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