15 Photoperiodism in Insects and Other Animals

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Abstract: Many animals, particularly those living at higher latitudes, use information from day length (or night length) to regulate seasonally appropriate behavioral and developmental strategies. The most common of these are the onset of overwintering diapause in the insects, and seasonal breeding strategies in many animal groups. This chapter examines the role of light in these processes: the photoreceptive “input pathway” to the photoperiodic clock, whether that clock is a function of the circadian system, its relationship to overt behavioral circadian rhythms and, in insects, its endocrine output to diapause or continuous summer development. Major models for the photoperiodic clock are described and evaluated, particularly whether apparent hourglass-like responses represent a distinct non-circadian clock or merely a variant of a circadian-based mechanism in which constituent oscillators “damp” rather rapidly in extended periods of darkness. Finally, some recent developments in unraveling the molecular genetics of the photoperiodic response are described.

15.1. Introduction

Soon after Garner and Allard’s (1920) seminal paper on plant photoperiodism, similar observations were made on animals. The first was by Marcovitch (1923, 1924), who observed that the appearance of seasonal morphs in several species of aphids was controlled by day length. The strawberry root aphid, *Aphis forbesi*, for example, produced sexual forms when natural summer days were restricted to seven hours. Conversely, long exposure to artificial light in September inhibited the sexual forms and induced viviparous reproduction typical of the summer. The first papers on the now enormous literature on the photoperiodic induction of insect dormancy (diapause) were those by Kogure (1933) and Sabrosky et al. (1933). Kogure’s work on the commercial silkworm *Bombyx mori* was a pioneer in many ways, including observations on light intensity thresholds and spectral sensitivity of the response. Photoperiodic responses have also been
described for other arthropods such as crustacea (Stross and Hill 1968), ticks (BelozeroV 1964) and mites (Lees 1953; Veerman 1977); also for other invertebrate phyla such as molluscs (Joosse 1984; Wayne 2001). Among the insects, photoperiodic induction of diapause has been demonstrated in over 500 species from 15 orders (Nishizuka et al. 1998) and must be considered widespread if not almost universal amongst those species living at higher latitudes (Saunders 2002).

Similar day length–dependent effects have been described in vertebrates. Rowan (1926) was the first to show that day length could have important effects on reproduction and behavior of birds (see Dawson et al. 2001). Many species of mammals, too, time their seasonal cycles of breeding by using a photoperiodic response (Baker and Ranson 1932; Bissonnette 1932; Goldman 2001). More limited information is available for “lower” vertebrates, such responses being known for fish, amphibia and reptiles (Underwood and Goldman 1987).

The selective advantages afforded by these photoperiodic responses are both clear and profound. Most animals restrict their physiologically “active” stages, such as growth and reproduction, to those times of the year when food supplies are abundant and climatic conditions are amenable for growth and development. At higher latitudes, therefore, most insects restrict such activities to the warmer months, and the winter is passed in a state of dormancy (diapause) induced, in most cases, by the shorter days of autumn. Among the vertebrates, birds build their nests and lay eggs as days increase in the spring so that the hatchlings are assured of a plentiful supply of food. For similar reasons, mammals also tend to give birth in the spring, those with a short gestation period such as rodents becoming sexually mature as the days lengthen, whereas those with a longer gestation, such as sheep or deer, become sexually active in the autumn. In all cases photoperiodic responses provide seasonally appropriate strategies ensuring maximum survival.

The literature on animal photoperiodism is now very large and cannot be covered adequately in a review of this length. For this reason emphasis will be on the insects, with reference to work on other taxa, particularly birds and mammals, given where appropriate. Particular attention will be paid to the photobiology of the response, and to the contentious question whether the time measurement inherent in insect photoperiodism is provided by components of the circadian system or by some form of nonscillatory hourglass-like mechanism. Much of the work on insect photoperiodism is still at the stage of physiological experimentation and model building, with modern genetic and molecular investigations lagging behind those of closely related fields such as circadian rhythmicity (see Chapter 14). Here it should be noted that the “genetic” insect of choice—the fruitfly Drosophila melanogaster—presents only rudimentary photoperiodic responses (Saunders et al. 1989), unlike its robust daily rhythms of locomotor activity and pupal eclosion which have greatly facilitated analysis of the insect circadian “clock.” Until a more congenial model for photoperiodism is forthcoming, analysis of the very complex processes involved in seasonal phenomena will be severely hampered.