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Action Spectra for Photoperiodic Response in a Diapausing Mosquito

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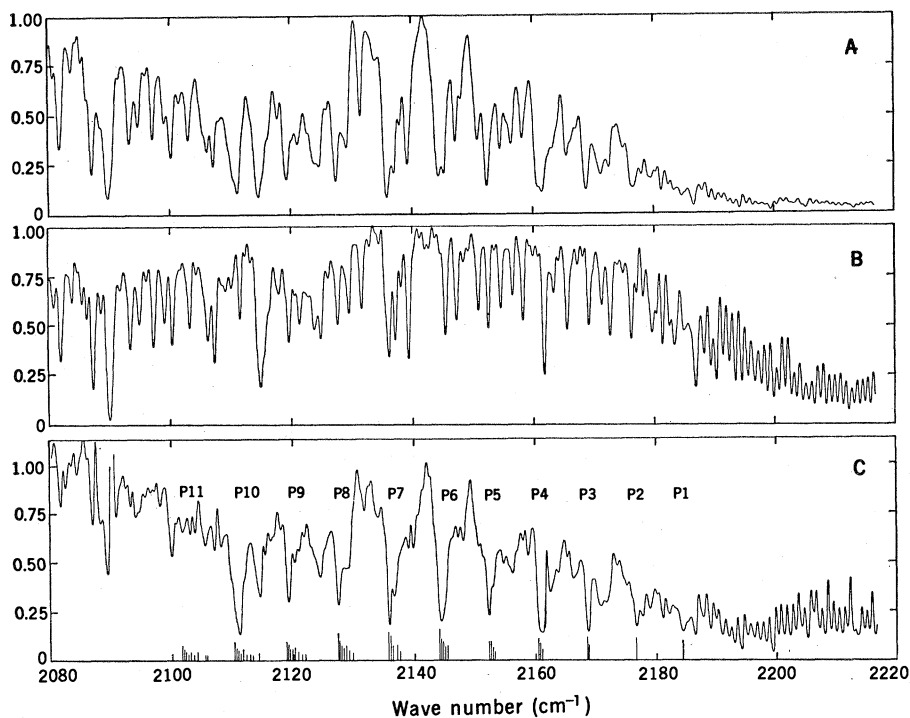


Fig. 1. The spectrum of Jupiter (A), the spectrum of the sun (B), and a ratio of the spectrum of Jupiter to that of the sun (C). The ordinates are given in arbitrary units. At the base of the spectrum in (C) are marked the individual components of the J-manifolds (2); the intensities are representational only. Furthermore, the ratio has not entirely eliminated the effect of telluric absorption, because the telluric air mass in the solar spectrum is significantly less than that for Jupiter.

none of the observed lines (as we shall call the unresolved manifolds) is free of telluric blending. Figure 1 shows some of the lines and a comparison solar spectrum.

This spectral region is strongly absorbed by Earth's atmosphere. Among the most evident absorptions are the center of the 1-0 CO band, the high-frequency wing of the 6.3- $\mu$  H<sub>2</sub>O bands, the P-branch of the  $\nu_3$  N<sub>2</sub>O band, and the low-frequency wing of the 4.2- $\mu$  CO<sub>2</sub> bands. In particular, the N<sub>2</sub>O and CO<sub>2</sub> bands are so strong that all trace of the CH<sub>3</sub>D Q- and R-branches disappears. Nevertheless, for all the P-branch from P2 to P11, there is a jovian line absorption in a position appropriate to each of the manifolds.

It is not possible, at the present time, to give either a CH<sub>3</sub>D abundance or a D/H ratio. The determination of the CH<sub>3</sub>D abundance will require a detailed experimental and theoretical consideration of line-formation in the jovian atmosphere under conditions wherein both thermal emission and solar reflection may be important. The D/H ratio will, in turn, be very model-dependent because first the CH<sub>3</sub>D/CH<sub>4</sub> ratio must be determined and the CH<sub>4</sub> abundance can be found only from examination of overtone bands at much higher frequency. Because of its great strength, the nearby  $\nu_3$  CH<sub>4</sub> band at 3.3  $\mu$  is virtually unobservable in the jovian atmosphere (3). The 4- to 5- $\mu$  window of the at-

mosphere of Earth roughly coincides with a window in the jovian atmosphere. The jovian window occurs in the interval between the  $\nu_4$  ammonia band centered near 1627 cm<sup>-1</sup> and the  $\nu_3$  methane band centered near 3020 cm<sup>-1</sup>. Both of these bands are very strong so that the resultant window is only a few hundred reciprocal centimeters wide. The  $\nu_1$  CH<sub>3</sub>D band, fortunately, falls within this window but the effective depth of the jovian atmosphere is much greater at these frequencies than at higher frequencies

## Action Spectra for Photoperiodic Response in a Diapausing Mosquito

**Abstract.** While 540 nanometers is the most effective wavelength in provoking development, larvae are far more responsive to 540-nanometer light if it is provided immediately preceding rather than following a white-light photophase which otherwise serves to maintain diapause. This difference in sensitivity is probably due to bleaching and implies that the larvae experience an asymmetric day.

Last-stage larvae of the nonbiting mosquito, *Chaoborus americanus*, overwinter in a state of developmental standstill which is provoked (1) and sustained by exposure to short-day conditions. When overwintering larvae are collected from the shallow ponds in which they often abound, the diapause persists if the larvae are maintained under short-day conditions at 5°C or at room temperature. By contrast, the larval diapause is terminated, and pupa-

(shorter wavelengths). The great strength of the CH<sub>3</sub>D band is therefore only apparent, and it should not be construed that the D/H ratio is necessarily much greater than on Earth.

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4. This paper presents the results of one phase of research carried out at the Jet Propulsion Laboratory under NASA contract NAS7-100.

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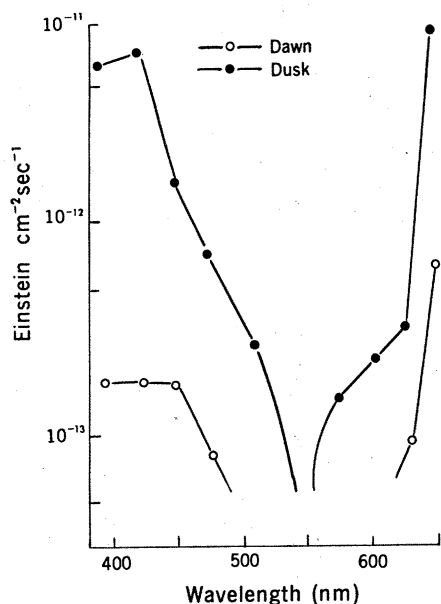


Fig. 1. Action spectra for photoperiodically provoked termination of diapause. The curves represent the flux density of quanta necessary to elicit 50 percent development when provided in 4-hour pulses either immediately preceding (dawn) or immediately after (dusk) a 12-hour white-light photophase.

of near-monochromatic light (4) of controlled intensity (5), provided either immediately before or after the white-light short-day regimen. Each wavelength was tested at a series of flux densities. After 5 or 7 days of treatment at  $23^{\circ} \pm 1.5^{\circ}\text{C}$ , all individuals were returned to the white-light short-day regimen (LD, 12:12) and starved at  $23^{\circ} \pm 1.5^{\circ}\text{C}$  in the absence of food. Five days thereafter, the termination of diapause was scored in terms of the initiation of pupal development, as signaled by the appearance of the pupal breathing horns. All experiments were performed in parallel with long- and short-day controls which received only white light (16 or 12 hours, respectively). During the several months required for the experiments here reported, 44 to 91 percent of the long-day controls showed development; the corresponding data for the short-day controls ranged from 0 to 8 percent. The percentage of development was calculated relative to these controls. A dose-response curve was ordinarily plotted for each wavelength and the 50 percent intercept was read directly from it.

The action spectra for the 50 percent developmental response are shown in Fig. 1. The spectra at dawn and at dusk appear to be qualitatively similar, the most effective wavelength being yellow-green light at 540 nm. However, at all wavelengths there are impressive quan-

titative differences between the two curves in that the insects' sensitivity at dawn is about an order of magnitude greater than at dusk. At the most effective wavelength of 540 nm the sensitivity of the larvae, both at dawn and at dusk, exceeded the limits of the photocells ( $5 \times 10^{-14}$  einstein  $\text{cm}^{-2} \text{sec}^{-1}$ ). This latter value approximates the experimentally determined "dusk" sensitivity at 540 nm in that it provoked 53 percent development. Qualitatively similar, but quantitatively different action spectra were obtained when the data were computed for "threshold response" and "saturating response." At each wavelength the threshold responses required flux densities about an order of magnitude less, and saturating responses about an order of magnitude greater, than the 50 percent response.

*Chaoborus* larvae are remarkably transparent, the only obvious pigment being in the eyes and swim bladders. The cuticle, for example, is completely devoid of any pigment that might exert a filtering action on incident white light. Consequently, the action spectra (Fig. 1) suggest that light reception is by a red pigment with a strong absorption maximum at 540 nm. This value is substantially higher than that reported for most other insects where maximum sensitivity is in the blue, with a virtual cutoff at about 500 nm (6, 7). A notable exception is the pink bollworm (*Pectinophora gossypiella*) in which blue (480 nm) and red (640 nm) are equally effective in provoking or averting the onset of larval diapause. Red light was, by contrast, completely ineffective in synchronizing the oviposition, hatching, and adult ecdysis of this moth (8).

A comparison of spectra at dawn and at dusk has apparently not been reported for any other animal. The most pertinent previous study is that carried out by Lees on the aphid *Megoura viciae* (6, 9). Lees presents an action spectrum of effective wavelengths introduced  $1\frac{1}{2}$  hours after the lights were turned off. Sensitivity extended throughout the blue and blue-green with a pronounced maximum from 450 to 470 nm. Lees reports preliminary findings of experiments in which the night was interrupted shortly before dawn. The wavelength of maximum effectiveness continued to be in the blue at 470 nm, but the action spectrum included somewhat higher wavelengths. Consequently, it would appear that the aphid makes use of a different photosensitive pigment from that used by *Chaoborus*.

The foregoing data constitute a novel finding—namely, a tenfold greater photosensitivity at dawn than at dusk. Since these mosquito larvae apparently make use of the same pigment for the reception of light at dawn and at dusk, the change in sensitivity can be most simply accounted for by the assumption that the pigment is subject to partial bleaching during prolonged exposure to light. Under that circumstance, dawn would find the receptor mechanism in the dark-adapted state, whereas the higher thresholds at dusk would be directly attributable to a less efficient absorption of light by the partially bleached pigment of the light-adapted mechanism. The net effect is that a "day" to these larvae is asymmetric in that it begins substantially before sunrise but terminates soon after sunset.

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4. White light was provided by a circulating water-cooled 15-watt tungsten lamp at a distance of 3 to 10 cm. Spectral light was achieved with Balzers second-order interference filters incorporating glass primary and tertiary cutoff filters. Peak transmission was checked with a Beckman DU spectrophotometer. Half widths ranged from 10 to 20 nm (420- to 630-nm filters) to 25 to 40 nm (390- and 660-nm filters). Sources included medium-pressure mercury vapor and tungsten filament lamps. Intensity was regulated by interposition of neutral density filters (Kodak Wratten No. 96 or Wipette tissues, or both). Fine control was achieved by partial crossing of polarized sheets (Kodak Pola-Screen) set between the neutral density filters and the animals.
5. Nonlinear cadmium sulfide photocells were calibrated with a linear silicon solar cell (Hoffman Electronics EA1) in conjunction with a Keithly microvoltmeter, which was in turn calibrated with a blackbody radiometer (Yellow Springs Instrument). Each cadmium sulfide photocell was individually calibrated with a specific interference filter and specific experimental jar. This method permitted control of intensity from approximately  $5 \times 10^{-14}$  to  $5 \times 10^{-10}$  einstein  $\text{cm}^{-2} \text{sec}^{-1}$  with an estimated absolute accuracy of about half an order of magnitude and an estimated relative accuracy of about 0.1 to 0.3 of an order of magnitude.
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