

The significance of moonlight in photoperiodic responses of insects

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Introduction

Photoperiod, as it affects insects, is usually taken as the time between sunrise and sunset. Its effects are more apparent in temperate zones, where it varies much, than near the equator, where it varies little. The fact that in the tropics the moon sometimes produces enough light to lengthen the photoperiod considerably, even up to 24 h, has been overlooked, together with possibly important biological consequences.

Illumination during the lunar cycle

Figure 1 shows how the light from a full moon affects photoperiod at Kampala, Uganda, taking 0.2 lx (Minnaert, 1954; Kimball, 1916; Explanatory Supplement, 1961) as the illumination at full moon and allowing for extinction (the loss of light during its passage through the atmosphere) at each degree of the moon's elevation up to 45°, beyond which extinction is considered to be constant. A full moon provides about the same illumination at zenith as at 30 min after sunset (about civil twilight) on a clear moonless evening. After sunset, on a moonless night, the light decreases by almost five orders of magnitude in an hour, but when the moon is up, the change is much less. Figure 2 shows that the situation on nights immediately after full moon is very different; on the night after full moon the change to constant illumination occurs slightly later, about 45 min after sunset, and to less illumination. The next night, illumination increases rapidly from about 0.01 lx about 50 min after sunset, but on the third night after full moon it decreases to that of starlight (0.0009 lx (Kimball, 1916)) before moonrise, and then increases rapidly but does not attain 0.1 lx.

Illumination of 5 lx has been cited as a common lower threshold of intensity for diapause induction (Beck, 1968), but some insects respond to much smaller intensities. For example, *Leptinotarsa decemlineata* (Say) responds to any white light intensity over 0.1 lx, with increasing response up to 5.0 lx, and it has been suggested that the light of full moon "may act as a supplement to the daily photoperiod" (de Wilde & Bonga, 1958) (the opposite view has also been expressed—Lees (1955)), and light intensities simulating moonlight (0.02–0.10 lx) are effective as time cues for metamorphosis and swarming in the Nereid *Platynereis dumerilii* (Hauenschild, 1960). The possibility that changes in illumination during the period at and near full moon act as photoperiodic cues for some behavioural and physiological changes in some insects should not, therefore, be neglected. In each lunar cycle there is a period of 4–6 days, including two days before full moon, when illumination is brighter than 0.1 lx for 20 or more hours in each 24-h period, and there is a 48-h period (including night of full moon and the night following) when illumination is continuously above 0.1 lx. If this intensity is accepted as critical, then in every lunar cycle, beginning at new moon, photoperiod changes from a light-dark ratio (LL:DD) of 12:12 to about 20:4, and then to 24:0. This is followed quickly by a period of minimum light intensity of increasing length. In equatorial areas these changes

occur over a short period and are repeated each month so they constitute periodic events that could provide cues for insects. They are also the equivalent of experimental schedules which introduce a continuous photophase into a pre-existing LL:DD regime, followed by the re-introduction of a scotophase. In this type of schedule, LL:DD LL:LL LL:DD, it is well established that the continuous photophase disentrains established rhythms which are re-entrained by the subsequent scotophase. In species in which the cue is light-off, or the light-dark change, there is often a greater response to the second light-dark change after the period of continuous illumination, because time is required for synchronising all the individuals in the population to the new regime, e.g., in the oviposition cycle of *Aedes (Stegomyia) aegypti* (L.) (Gillett, 1971).

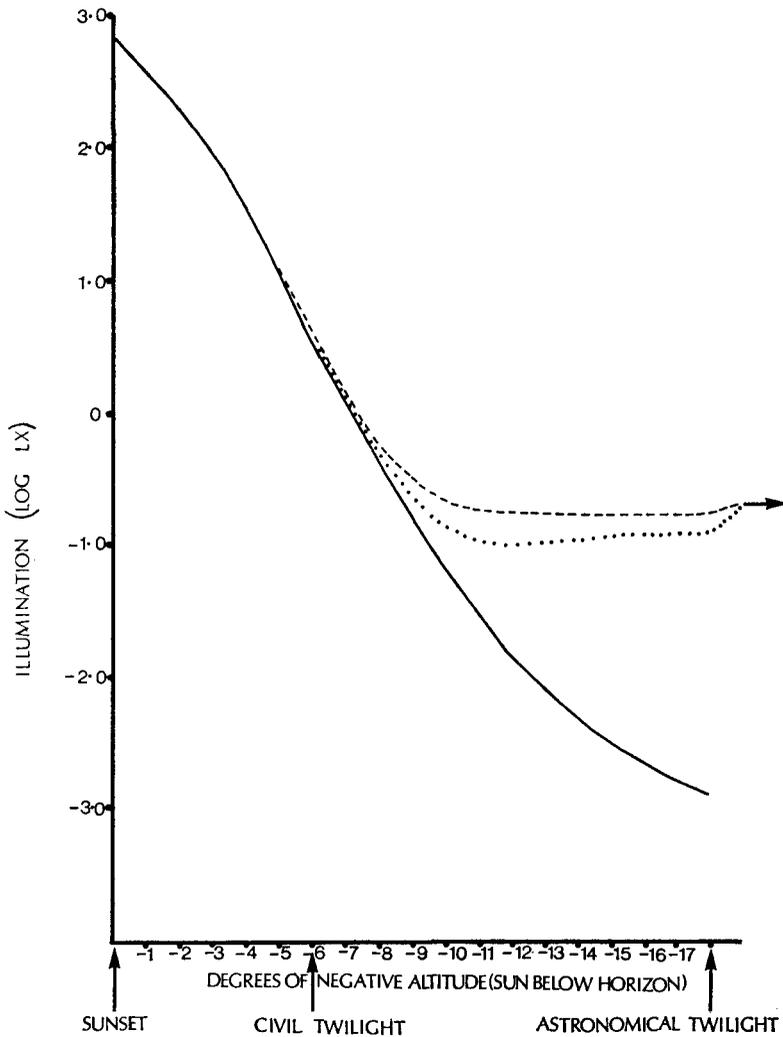


Fig. 1.—Effect of full moon on twilight illumination, based upon times at Kampala, Uganda, $0^{\circ}32'N$. (Solid line, twilight illumination without moon; dashed line, twilight illumination with full moon rise 46 min before sunset; dotted line, twilight illumination with full moon rise 8 min after sunset.)

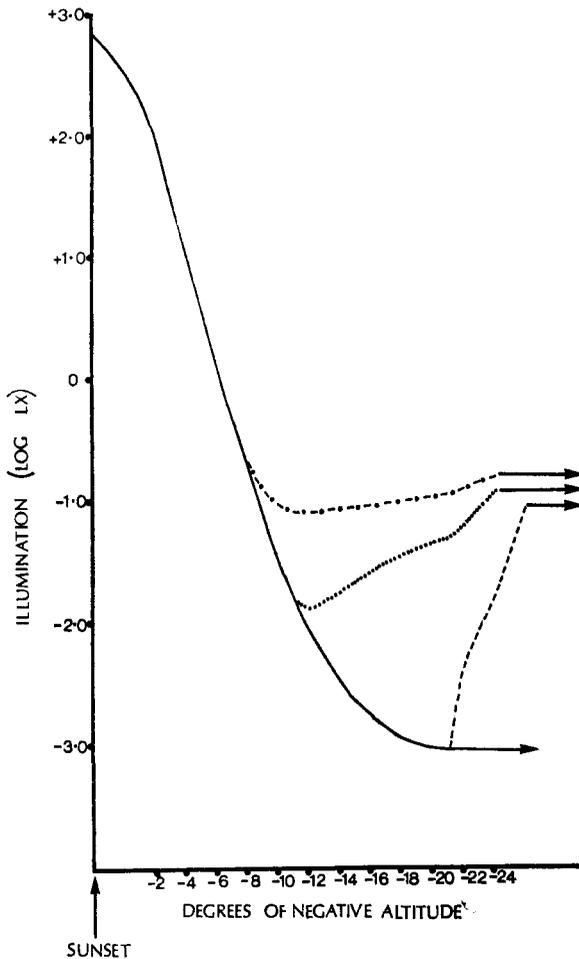


Fig. 2.—Effect of moon on twilight illumination on nights following full moon, based on average times of moonrise, Kampala. (Solid line, twilight illumination without moon; dash-dot lines, illumination on night after full moon; dotted line, illumination two nights after full moon; dashed line, illumination three nights after full moon.)

Possible examples of lunar rhythm in insects

A comparable event in the field is that recorded by Nemeč (1971) of a peak of oviposition of *Heliothis zea* (Boddie) immediately after full moon (not, as the author erroneously states, at new moon—see Fig. 3). *H. zea* is inhibited from flight by brighter light than 0.1 lx (Nemeč, 1971) and its pattern of egg laying is not a generation cycle as has been suggested (Nemeč, 1971), but can be explained as a re-synchronisation of oviposition induced by the dark periods during the early parts of the nights after the period of continuous light at full moon. Light-trap captures of *H. zea* show the same type of response (Fig. 3).

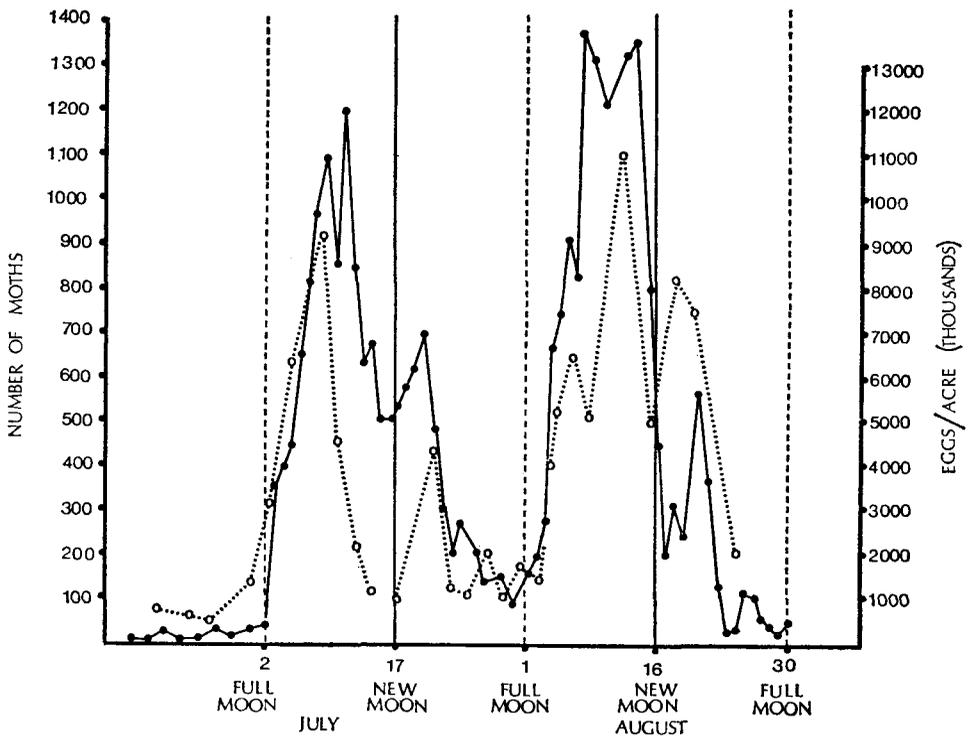


Fig. 3.—Combined nightly catches of moths of *Heliothis zea* in two light-traps, bollworm egg numbers in cotton, and lunar phases, 1966; redrawn from Nemeč (1971) with markers at new moon and full moon. (Open circles, eggs/acre; closed circles, moths/trap.)

Alam & Hudson (1969) recorded numbers of adults of *Diatraea saccharalis* (F.) on the kitchen walls of a house in Barbados. They concluded that maximum numbers occurred at new moon but their data show that most were found several days before new moon (Fig. 4). Fisk & Perez (1969) observed that, in a Puerto Rican population of *D. saccharalis*, black-light traps collected female moths only on nights with little or no moonlight, whereas male moths were taken by the same traps in greater numbers on nights of full moon. The females had a single peak of flight activity, near 22.00 h, while the males had two peaks, one near 23.00 h, the second at about 04.00 h. These observations suggest that, as with *H. zea*, females of *D. saccharalis* are inhibited from flight by bright moonlight and that the maximum catch in Fig. 4, between full moon and new moon, is caused by re-synchronisation of the flight activity of females by the dark periods of the early part of the nights after full moon. The males are not inhibited and the fall in the Barbados catch at full moon is caused by the reduced efficiency of the house lights at full moon, so that fewer males were caught, and by the cessation of flight by female moths. Similar responses are also evident from light-trap catches of *Mantispa* spp. (Neuroptera) and *Schalidomitra variegata* (Holland) (Lepidoptera, Noctuidae) at Kawanda Research Station, Kampala, Uganda (Fig. 5), which show a rapid increase of catch on the nights immediately after full moon, to numbers well above those at new moon when, as Williams (1936) and Provost (1959) suggested, light-trap catches might be expected to be greatest. Photoperiodism controlled by the amount, duration and

distribution of moonlight may, therefore, be widespread in insects, at least in the latitudinal belt between the tropics, and could form the basis for predicting such behaviour patterns as peak periods of oviposition or of emergence.

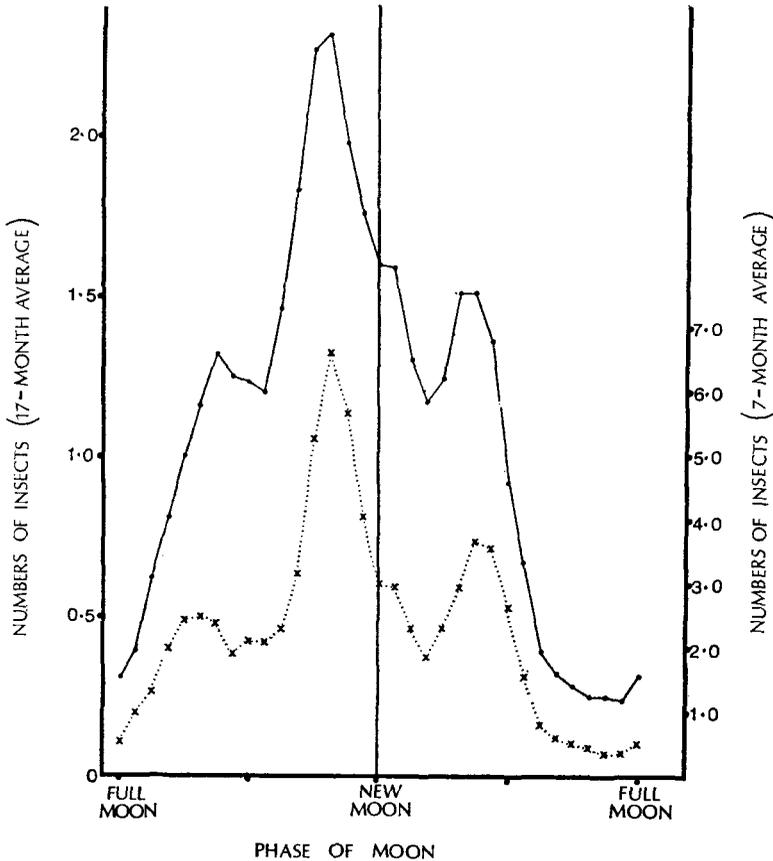


Fig. 4.—Mean catches of *Diatraea saccharalis* in relation to phase of moon, Barbados, 1965-67; data from Alam & Hudson (1969). (Solid line, mean catch over total period of 17 months; dotted line, mean catch for first seven months. For details of the methods used for analysis of light-trap catches in relation to moon phase as in Fig. 4-5, see Bowden (1973).)

The change in twilight illumination caused by a full moon may also be expected to affect crepuscular activities such as swarming. Swarming of male mosquitoes is believed to cease when illumination sinks to a critical intensity (Haddow & Corbet, 1961; Nielsen & Nielsen, 1963), which may be about 1% of illumination when swarming begins (Nielsen & Nielsen, 1963). For some species, on evenings at and near full moon, swarming will not be prevented by dim light, but will continue, once it has begun, until exhaustion or some other factor stops it. In the mosquito *Psorophora confinnis* (Lynch Arrib.) swarming continued on the night of full moon for at least an hour beyond the usual time, because illumination did not fall to the critical level of 0.02 lx (Provost, 1958).

Probably the periods of activity of diurnal species can also be extended by moonlight in both morning and evening twilights.

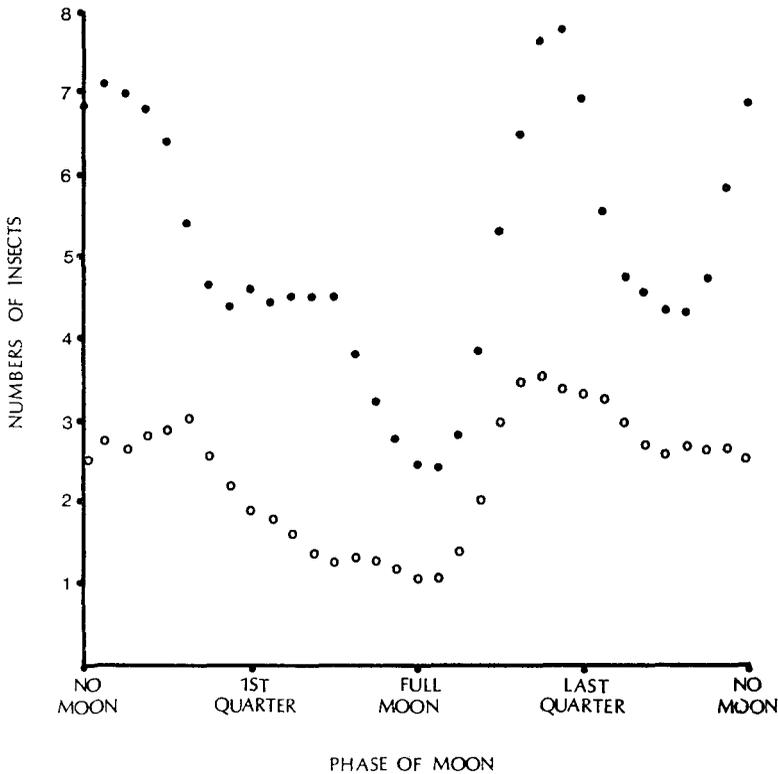


Fig. 5.—Mean catches of *Schalidomitra variegata* and *Mantispa* spp., in relation to phase of moon, Kawanda Research Station, Kampala, Uganda, 1958–62. (Open circles, *Mantispa*; closed circles, *S. variegata*.)

Lunar rhythms in insects have previously been recorded only in species whose life-history is wholly or partly aquatic: Ephemeroptera (Hora, 1927; Hartland-Rowe, 1955, 1958), Belostomatidae (Bowden, 1964); Chaoboridae (Macdonald, 1956) and Chironomidae (Macdonald, 1956; Caspers, 1951; Fryer, 1959), but, contrary to the suggestion of Williams *et al.* (1956), they may in fact be widespread and very important in insect behaviour and ecology and, therefore, in control programmes.

Summary

In the tropics, the amount and the pattern of distribution of moonlight at and just after full moon produces alternating periods of continuous illumination and darkness which could provide photoperiodic cues for insects. Examples of possible photoperiodic effects induced by moonlight, taken from the published literature, include the flight activity and oviposition patterns shown by females of *Heliothis zea* (Boddie) and *Diatraea saccharalis* (F.) and crepuscular activity of mosquitoes. It is suggested that photoperiodic

responses to moonlight could form the basis for a simple method of predicting such events.

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