Asymmetry in Eocrepuscular Diel Periodicities of Insects

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In certain insects there exist eocrepuscular diel periodicities of activity in which the sunrise peak occurs at a higher light intensity than does the peak at sunset. This may happen because the indicator-process chosen by the observer to designate the activity is not the first in a behavioural sequence released by light of a critical intensity.

Insects of several species are briefly and intensely active twice each day, once near sunrise and again near sunset. This type of diel periodicity, which may involve flight, swarming, feeding or arrival at light, has been termed 'eocrepuscular' (Haddow 1945). It is encountered more often in tropical than in temperate regions, perhaps because air temperatures at dawn are more frequently permissive at lower latitudes. A characteristic of eocrepuscular insects is that their activity is confined within a predictable range of light intensities. Thus it has been supposed that such activity is positioned mainly exogenously, by light thresholds.

This view has been confirmed experimentally for *Culex pipiens fatigans* Wied. by Nielsen and Nielsen (1962). The eocrepuscular swarming of this mosquito occurs only within a certain range of light intensity. Within this range it can be induced at any time by a slow light change (increasing or decreasing) as long as temperature is favourable, and more than five hours have passed since the last light change. The greatest proportion of males participate in swarms under the widest range of light intensity if the temperature is 24–25° C. and if the preceding light change lasted for more than 20 minutes. The light thresholds at which swarming begins and ceases depend, *inter alia*, on the rate of light change beforehand. Sunrise swarms of this mosquito are delayed slightly with increasing temperature. Sunset swarms begin and sunrise swarms end at the same light intensity. In the Nielsens' experiments there was an indication that an urge to swarm preceded its exogenous release at sunrise; but the fact that it can be induced outside its accustomed time, or made to continue for hours (instead of minutes) if the intensity is held experimentally at a permissive level, demonstrates that its temporal pattern is determined exogenously. That an orderly change of light intensity is a prerequisite for swarming shows that the concept of a simple threshold needs elaboration here. Evidently some processes, activated by light, must be completed before swarming can begin. This suggests an explanation for the asymmetry observed in diel periodicities of certain mosquitoes, caddisflies and mayflies.

The biting periodicity of the mosquito, *Mansonia fuscopennata* (Theo.), at the margins of forest near Entebbe, Uganda, shows two well-defined peaks, one after sunset and the other before sunrise, each being associated with a certain light intensity. The sunrise peak, however, consistently occurs at a higher light intensity than the one at sunset (Haddow 1964). The same kind of relationship obtains between peaks of arrival at a light-trap of the eocrepuscular caddisfly, *Cheumatopsyche copiosa* Kimmins (Corbet and Tjønneland 1955). Expressed in values of crep (Nielsen 1963), the sunset peak on four comparable nights at Jinja, Uganda, occurred at about 1.80 and the sunrise peak at at 1.06. In clear weather these times would correspond to intensities of $\bar{2}.85$ and 0.4 log lux respectively. In the mayfly, *Cloëon dentatum* Kimmins, the two peaks of arrival at light are

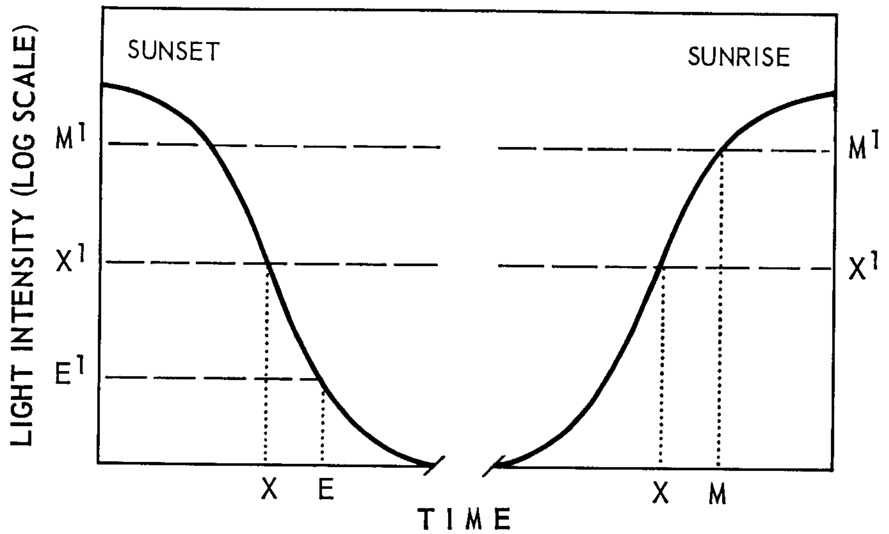

Fig. 1. Diagram illustrating the way in which a sunset activity peak (at time E) can fall at a lower light intensity than a sunrise peak (at time M) in an eocrepuscular periodicity. Evening and morning, the activity sequence is released at time X (light intensity X′); the overt expression of it, or the indicator-process used by an observer, occurs after a constant delay shown as XE or XM on the abscissa. Thus visible activity occurs at a lower intensity (E′) in the evening than in the morning (M′). The intensity (X′) releasing the sequence lies between E′ and M′.

disposed in almost exactly the same way (Tjønneland 1960). In all three insects the morning peak falls approximately 20 minutes later than would be expected were it to occur at the same light intensity as its evening counterpart.

The asymmetry of these tropical periodicities is unlikely to be simply a a temperature effect: lower (sunrise) temperatures cause light thresholds for the onset of swarming to fall in *Culex pipiens fatigans* (Nielsen and Nielsen 1962). It may merely reflect the fact that the 'indicator-process' used to define the periodicity (*viz.* arrival at bait or at light) is not itself initiated by changing light intensity, but occurs as a consequence of others that are so initiated. If these other, prerequisite processes need a detectable time for completion, and begin at the same intensity morning and evening, then the sunrise peak can always be expected to occur relatively later than the sunset peak. Furthermore, according to this hypothesis, the difference between the crep values at which the two peaks occur will be equivalent to twice the time needed for completion of the exogenously controlled processes which precede the observed activity (Fig. 1). Thus, in the mosquito, caddisfly and mayfly, it might be supposed that the time which elapses between initiation of the sequence, and arrival at bait or light is about 10 minutes (*ca* 0.5 crep). Consistent with this interpretation for *Mansonia fuscopennata* is that the sunset biting wave at forest margins—as in *M. perturbans* (Walk.) (Snow 1955)—is evidently due mainly to the interception of females in transit, and is prefaced by a movement from ground layer to canopy (Haddow 1964) similar to the ascent which precedes evening swarming or migration in many other mosquitoes (see Nielsen and Nielsen 1958). If, as is very likely, this ascent is initiated exogenously by light intensity, and if it takes a detectable time, then this alone could result in the sunrise peak falling at a lower value of crep than the sunset peak.

The observed asymmetry could doubtless be caused in other ways. The purpose of this note is to point out that the indicator-process chosen by an observer to designate an activity is not necessarily the first in a self-contained behavioural sequence initiated by exogenous factors. If others precede it, there will necessarily be a delay between initiation of the sequence and the overt manifestation of it to the observer. The existence of a close correlation between an indicator-process and current light intensity makes it highly probable that the relevant behaviour sequence is initiated exogenously; but it does not necessarily reveal the time or intensity at which the initiation takes place. This can only be found by experiment—or perhaps inferred from asymmetrical distributions of the kind described here.

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