

Cd by a sublimation mechanism at ambient temperatures. This is not to imply, however, that such processes could not be important at higher temperatures or lower atmospheric pressures, possibly contributing to the atmospheric chemistry of other planets.

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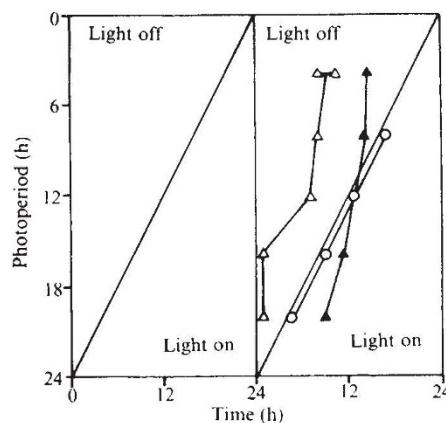
## Control of flight activity in mosquitoes

JONES, in his interpretation of the activity cycle of the mosquito *Culex pipiens fatigans* Wied. in constant light (LL) following a light : dark (LD) regime of 12 h light and 12 h dark<sup>1</sup>, stated that it was possible to calculate that the first peak should have occurred about 18 h after light-on or 6 h after the normal time of light-off. In his recordings of activity the main peaks in LD 12:12 were immediately following light-off and light-on. In most field observations of biting activity<sup>2–4</sup>, in the laboratory cycle of mating activity<sup>5</sup> and in my laboratory observations of flight activity, the main peaks in the day-length (LD 12:12) typical of the tropics are around midnight and after light-on. By plotting the positions of the peaks in various LD regimes I found the control of flight activity in *C.p. fatigans* to be a combination of light-on some 13–18 h earlier and light-off some 8–14 h earlier (Fig. 1). The mosquito will also respond immediately to light-on in LD 8:16 to LD 20:4. I did not study the activity in LL but in constant dark (DD) following an LD 12:12 I observed a bimodal cycle with one peak following light-on by about 18 h and the other following light-off by about 12 h; these were both repeated twice in DD with a period of about 27 h. Clear double peaks were shown in DD following an LD 4:20 rearing regime; the period in this case was about 24 h. The second peak became much greater with successive cycles to present a result resembling the activity in LL as recorded by Jones<sup>1</sup>.

The separate phase-setting effects of light-on (dawn) and light-off (dusk) in a mosquito were first observed for *Aedes*

*aegypti* L. and formed the basis for suggesting an association between the range of photoperiods in which these separate phase-setting effects reinforce each other and the photoperiod usually encountered by a species throughout its natural range<sup>6</sup>. For dark-active species, such as *Anopheles farauti* Laveran, the optimum photoperiod seems to be determined by the coincidence of a peak entrained by the previous light-off and the peak in response to light-on<sup>7</sup>. *C.p. fatigans*, to judge from the increase in the size of the light-off entrained peak in DD and LL, probably has the same mechanism for determining photoperiod. A theoretical optimum daylength of 12–14 h for *C.p. fatigans*, derived from Fig. 1, compares reasonably well with its known geographical range of 0°–35/40° latitude.

The relevance of the association between photoperiod measurement and the photoperiods within their natural geographical range is not obvious for tropical mosquitoes but increasingly in recent years separate 'dawn' and 'dusk' oscillations have been linked with the



**Fig. 1** The positions of the peaks of activity of *C.p. fatigans* relative to light-on and light-off when the mosquitoes are in different light regimes. Diagonal lines divide light-on and light-off periods. Peaks of activity are indicated as: ○, peak at light-on; △, peak following light-on by 13–18 h; ▲, peak following light-off by 8–14 h. Total of 26 individual females was studied; activity was recorded acoustically<sup>6</sup> at 25 °C; light intensity was 70 lx.

measurement of photoperiod by insects which have a diapause stage in the annual life-cycle<sup>8</sup>. It has not been clearly established, however, whether overt rhythms of activity can be used as indicator rhythms in photoperiodism studies. I have studied several temperate species of mosquito which have at least two generations per year. For *C. pipiens pipiens* L. I obtained graphs of activity peaks which for adults reared in July from larvae collected in southern England (latitude 51 °N, daylength 15 h), that is, a summer generation, gave a theoretical optimum daylength range of 14–17 h,

but for adults taken from hibernation in January, that is, the winter generation, the range was 11–12 h. *C. torrentium* Martini showed a range of 15–18 h for adults reared from larvae collected in mid-July whereas the range for adults reared from larvae collected in mid-September (daylength 13 h) was 12–14 h. The effect of shortening daylengths on summer generation mosquitoes and of lengthening daylengths on winter generation mosquitoes can clearly produce an imbalance between the internal mechanisms controlling flight activity, so there may be a link between overt flight activity rhythms and the photoperiodic mechanism controlling the adult diapause of hibernating mosquitoes.

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**JONES REPLIES**—Biting and mating depend on flight, but do not necessarily have to show the same pattern; all that is required is sufficient flight activity at the appropriate time. The cycle I have observed in *C.p. fatigans* provides such a permissive framework; it is also consistent with the pattern of flight activity measured in the field using window traps.

Taylor's results<sup>1,2</sup> could indicate an interesting difference in behaviour between strains (his material originated in Lagos). Confirmation of his results would be useful as the experiments he has quoted were all carried out at the same time using only one batch of insects which had been reared together.

'Dawn' and 'dusk' oscillators may indeed play an important part in the control of mosquito flight activity. This would fit in with the new model for circadian pacemakers proposed by Pittendrigh and Daan<sup>3</sup> which they describe as a 'clock for all seasons'.

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