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Geographical Range and Circadian Rhythms

WHILE studying the effect of different photoperiods on the circadian rhythm of flight activity in the mosquito *Aedes aegypti* (L.), I observed that within a certain range of photoperiods the phase-setting effects of light-on ("dawn") and light-off ("dusk") reinforce each other; the range over which this reinforcement occurs coincides with that of the photoperiod which is usually encountered by this species throughout its natural geographical range[1]. If these two phenomena are associated in *Ae. aegypti*, one would expect the association also to hold in other species. I have recently carried out tests on various species of mosquito, deriving theoretical geographical ranges from their circadian rhythms and comparing these with the actual known ranges. The fit was very close in almost every case.

The following species were used in these tests, each being selected in part on account of its availability but chiefly because of peculiarities in its geographical range and natural active periods: *Ae. aegypti* was chosen as a species usually active in the light; *Anopheles plumbeus* Stephens and *Ae. punctor* (Kirby) were chosen as crepuscular species; *An. labranchiae atroparvus* van Thiel, *An. farauti* Laveran, *An. stephensi* Liston and *Culex pipiens pipiens* L. were chosen as species usually active in the dark. Adult females were used in all the experiments and these were either reared from eggs in a regime of 12 h light and 12 h dark (LD 12 : 12) or trapped on me in the field.

Flight activity was recorded automatically using an acoustic technique[2], the experiments being carried out at 25° C with a light intensity of 70 lx. The mean results for each regime were plotted as a histogram of activity against time.

Fig. 1 shows the results obtained with one species, *An. farauti*. This species is active in the dark, and the histograms show three peaks of activity, a peak at light-off (●), a peak at light-on (○) and a peak following light-off by 11–13 h (▲). These peaks are also shown on the graph of photoperiod against time. The second and third peaks (○ and ▲) coincide when the light period is within a range of about 11–13 h. If this range is converted into latitude, on the basis of summer solstice daylengths[3], an experimentally derived geographical range of 0°–20° appears for this species. In fact the actual range of this species is

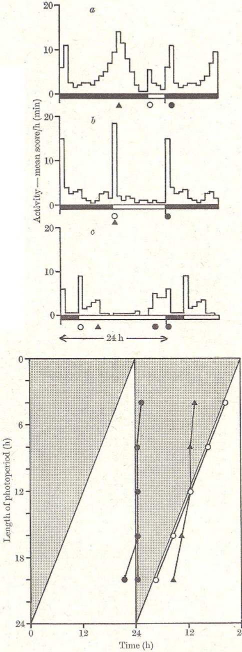

Fig. 1. The histograms show the flight activity of *An. farauti* in different light regimes. *a*, LD 4 : 20 ; *b*, LD 12 : 12 ; *c*, LD 20 : 4. Peaks of activity are indicated as: ●, peak at light-off; ○, peak at light-on; ▲, peak following light-off by 11–13 h. The graph shows the positions of the peaks of activity relative to light-on and light-off when the mosquitoes are in different light regimes.

0°–20° S (ref. 4). Under extreme photoperiods the position of the peak at light-off (●) is shifted: the peak is delayed in the LD 4 : 20 regime and advanced in the LD 20 : 4 regime. The relation between the first and third peaks (● and ▲) remains constant, as the third peak (▲) is also shifted. The timing of these peaks may be affected by light-on or possibly by the duration of light.

Table 1 shows the results of the survey and compares the experimentally derived range for each species with the actual range. Because the derived ranges are based on summer solstice daylength, the upper limits of latitude shown are of greater significance. In any given latitude the summer daylengths vary from about 12 h at the equinoxes up to the summer solstice maximum at that latitude. It will be noticed that there are certain anomalies in the results. The experimental range of *An. stephensi*, for example, is greater than the actual range. This can perhaps be explained by the fact that this species occurs in India and south-west Asia and the northern extent of its range is restricted by the physical barriers of the Himalayas (about 30° N) and the mountains of southern Turkey (37° N). *An. plumbeus*, *C. pipiens* and *Ae. punctor* were all obtained from field populations in southern England (51° N) and the experimental ranges suggest that the mosquitoes studied represent geographical races. Similar intraspecific variations have been recorded in studies of photoperiodism and geographical range[5].

Circadian rhythms seem to play a basic part in the adaptation of a mosquito species to its geographical range. It is not necessary to postulate whether the evolution of the timing system is a consequence of the photoperiods found at a given latitude or vice versa. The evolutionary origin of *Ae. aegypti* is thought to be in Ethiopia (6°–10° N) (ref. 6), but the species has spread throughout the world within the latitudes 0°–40°. Similarly, it is possible that *An. stephensi* originated in the Indian sub-continent (10°–30° N) and has spread round the coast of south-west Asia into Iraq (about 35° N), which is farther north than the Himalayas.

Table 1. COMPARISON OF RANGES DERIVED FROM THE CIRCADIAN RHYTHMS OF FLIGHT ACTIVITY IN DIFFERENT PHOTOPERIODS AND ACTUAL RANGES OF MOSQUITO SPECIES

Species	Experimentally derived range, °latitude	Actual range, °latitude
Light-active		
Ae. aegypti	0°–40°	0°–40°
Crepuscular		
An. plumbeus	47°–62°	40°–70°
Ae. punctor	30°–58°	45°–70°
Dark-active		
An. farauti	0°–20°	0°–20°
An. stephensi	0°–47°	10°–35°
C. pipiens	46°–57°	0°–60°
A.l. atroparvus	0°–55°	35°–55°

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B. TAYLOR

Department of Biology,
Brunel University,
London W3.

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