Diel periodicity in the landing of Aedes aegypti on man*

M. TRPIS,1 G. A. H. McCLELLAND,2 J. D. GILLET,3 C. TEESDALE,4 & T. R. RAO 6

The dynamics of transmission of disease agents by vectors depends, in part, on the probability of host-vector contact, which can vary with fluctuations of both host and vector. As important as seasonal variations is 24-hour periodicity in activity. Periodicity in the landing of males and females of Aedes aegypti on man has been assessed by means of catches of 15 hours or longer, with several persons as a bait. The assessments were made in a suburban area of Tanzania and continued throughout one year. Activity was observed to be almost entirely diurnal and diphasic. Whereas the detailed activity pattern of males agreed closely with that found elsewhere in East Africa, that of the females was unusual on account of the symmetry of the morning and afternoon peaks. Possible causes of differences among studies are discussed.

Periodic patterns in the activity of adult mosquitoes can profoundly influence the design of field experiments and the interpretation of catch data. They have epidemiological significance in terms of the varying probability of host-vector contact and are of fundamental interest to the student of biological rhythms. In the field, the subject has been studied principally by the 24-hour human-baited catch—a method largely developed by Haddow (1954). Most studies refer to what is termed the “biting-cycle”. However, data on non-biting males may be collected, and many female mosquitoes are caught before they have begun to feed. Although the intention of landing females may seem obvious, as many as 18% of A. aegypti females caught in this way have refused to engage subsequently (McClelland & Conway, 1971). Up to 41% of females that land have been found to be uninfested and much mating activity takes place on or near the host (Hartberg, 1971). Corbet (1966) has suggested that the term “cycle” be used only for a sequence of physiological or behavioural changes in an individual. Thus the term “biting-cycle” should be reserved for the pattern of feeding episodes usually correlated with the gonotrophic cycle in the individual female mosquito. Past and present work will therefore be considered in terms of periodicity in the rate of landing on a host (man).

A total of 17 series of timed baited catches of A. aegypti have been recorded by workers in East Africa (Teesdale, 1955, 1959; Lumsden, 1957; van Someren et al., 1958; and McClelland, 1959, 1960) and in West Africa (Boorman, 1960, 1961). In most of the series of catches, more than 85% of the landing activity of females occurred in the daytime or twilight, but at Newala, Tanzania, Lumsden (1957) found as much as 34% nocturnal activity in 2 series of catches and Teesdale (1955, 1959) recorded more than 26% in one-third of his series in Kenya. The relative importance of nocturnal activity in any particular locality remains to be assessed. In general, activity has been found to occur in fairly well-defined peaks. Lumsden (1957) noted as many as 6 such peaks, but his series were based on a single continuous catch of 49 hours, whereas, in the other studies, the results from several shorter catches over a longer period were combined. In 13 out of the 17 series of catches, including the 7 made away from the shelter of houses, most of the activity, or the largest peak, occurred in the afternoon or as late as the hour following sunset. However, among the house, verandah, or village series, the two of van Someren et al. (1958) in

---

* From the WHO East Africa Aedes Research Unit, Dar es Salaam, Tanzania.
1 Entomologist/Ecologist. Present address: Department of Biology, University of Notre Dame, Ind., USA.
2 Project Leader and Associate Professor of Entomology, University of California, Davis, Calif., USA.
3 WHO Consultant, Acting Project Leader, and Professor of Biology, Brunel University, Uxbridge, Middlesex, England.
4 WHO Consultant and Acting Project Leader.
5 WHO Consultant, Acting Project Leader, and Director, Virus Research Centre, Poona, India.
Table 1. Results of 14 collections of *Aedes aegypti* landing on man (hourly totals from 05.00 to 20.00 hours)

<table>
<thead>
<tr>
<th>Date of catch</th>
<th>Time of sunrise</th>
<th>Hours (East African Standard Time)</th>
<th>Total</th>
<th>Time of sunset</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>05 to 06</td>
<td>06 to 07</td>
<td>07 to 08</td>
</tr>
<tr>
<td>1 Jan. a)</td>
<td>06.18</td>
<td>7</td>
<td>40</td>
<td>13</td>
</tr>
<tr>
<td>22 a</td>
<td>06.26</td>
<td>3</td>
<td>30</td>
<td>15</td>
</tr>
<tr>
<td>19 Feb.</td>
<td>06.30</td>
<td>21 (0) b</td>
<td>66 (5)</td>
<td>52 (2)</td>
</tr>
<tr>
<td>26</td>
<td>06.30</td>
<td>10 (0)</td>
<td>113 (3)</td>
<td>20 (6)</td>
</tr>
<tr>
<td>5 Mar.</td>
<td>06.30</td>
<td>13 (0)</td>
<td>99 (1)</td>
<td>115 (21)</td>
</tr>
<tr>
<td>12</td>
<td>06.28</td>
<td>24 (0)</td>
<td>92 (7)</td>
<td>74 (9)</td>
</tr>
<tr>
<td>19</td>
<td>06.27</td>
<td>16 (10)</td>
<td>100 (11)</td>
<td>50 (14)</td>
</tr>
<tr>
<td>24 Apr.</td>
<td>06.24</td>
<td>-- c</td>
<td>124 (2)</td>
<td>28 (1)</td>
</tr>
<tr>
<td>27 May</td>
<td>06.27</td>
<td>-- d</td>
<td>45 (0)</td>
<td>22 (0)</td>
</tr>
<tr>
<td>25 June</td>
<td>06.34</td>
<td>-- d</td>
<td>16 (1)</td>
<td>34 (5)</td>
</tr>
<tr>
<td>21 July</td>
<td>06.35</td>
<td>10 (0)</td>
<td>13 (0)</td>
<td>11 (0)</td>
</tr>
<tr>
<td>26 Aug.</td>
<td>06.28</td>
<td>0 (1)</td>
<td>2 (2)</td>
<td>3 (0)</td>
</tr>
<tr>
<td>27 Oct.</td>
<td>06.01</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>2 (0)</td>
</tr>
<tr>
<td>26 Dec.</td>
<td>06.13</td>
<td>0 (0)</td>
<td>49 (2)</td>
<td>6 (1)</td>
</tr>
</tbody>
</table>

Totals females males

|                | 104 (11) | 779 (34) | 445 (59) | 163 (43) | 129 (32) | 125 (21) | 62 (26) | 53 (23) | 47 (31) | 120 (62) | 197 (38) | 310 (72) | 448 (87) | 508 (47) | 121 (11) | 3 611 (597) |

a Numbers of males not recorded.

b The figures in parentheses are the totals of males.

c This catch began at 06.00 hours and continued until 10.00 hours on 25 April (see Table 2). However, the data for the period 06.00–10.00 hours on 25 April were not used in calculating Mpc.

d These catches began at 06.00 hours and continued until 06.00 hours on the following day (see Table 2).

e A single female of *A. woodi* was included in this catch but the hour cannot be established.
Kenya and one each of those of Teesdale (1955, 1959) and Lumsden (1957) showed the most activity in the morning.

**LOCALITY AND METHODS**

The site—an automobile dump at Buguruni, a suburb of Dar es Salaam, Tanzania—was chosen in January 1969 after 5 months of trial catches in various parts of the city and environs. About 500 old motor-car bodies, scattered over an area of less than 1 ha and shaded by large trees, provided shelter for adult mosquitoes. The most common species present, *A. aegypti* (L.), *Culex pipiens fatigans* Wied., and *Toxorhynchites brevipalpis* Theobald, were breeding freely in the innumerable old tires that hold water in all seasons. During the rainy season, mosquitoes were present also in parts of car bodies and engines, discarded tins, snailshells, and treeholes, in which water had collected. The area was surrounded by well-built iron-roofed and mud-walled houses. Many people entered the dump at all times of the day, mostly to draw water at a well about 30 m from the catch site.

The dates of the catches are given in Table 1. During the first 3 months, 4-6 field assistants sat on a tarpaulin on the ground and caught mosquitoes landing on the exposed parts of their bodies. The remaining catches were standardized, 3 men sitting inside an orange-coloured canvas gable tent (2 x 2 x 2 m) one end of which was completely open (Trpis, 1962). The mosquitoes were placed in individual vials plugged with cotton wool, and each hour's catch was put in a separate bag. The men worked in shifts of up to 4 h under the continuous supervision of a senior assistant. One of us (M.T.) identified and recorded the material after the catch was completed.

In April, May, and June the catches began at 06.00 hours (East African Standard Time) and continued for 24 h or, on one occasion, for 28 h. The remaining catches began at 05.00 hours and lasted 15 h. The importance of adjusting the catch clock in relation to the exact time of sunset has been stressed by Haddow (1954) and Lumsden (1957). Sunrise is equally important in the present study, in which mosquitoes were active both early and late in the day. However, at a point 7° from the equator it is not possible to adjust the clock to both sunrise and sunset since the days vary considerably in length. The times of both sunrise and sunset have been calculated for Buguruni from the Nautical Almanac and are given in Table 1. The small range of variation is indicated on Fig. 1 by dotted lines.

In processing the results, “Williams’ mean” (*M*<sub>W</sub>) as defined by Haddow (1960) was used, since it generally gives the best measure of central tendency for this type of study (Haddow, 1954).

**RESULTS**

The results for the 15-h “day” from 05.00 hours to 20.00 hours are given for the entire year in Table 1. For clarity, the period from 20.00 hours to 10.00 hours in the 3 extended catches is given separately in Table 2. *M*<sub>W</sub> has been calculated for each hour of the “day” in the normal way. In the small series of catches for the “night” 20.00 hours to 05.00 hours, however, a 3-h running arithmetic mean was first computed for each hour of each catch and the *M*<sub>W</sub> was calculated from these smoothed values. The *M*<sub>W</sub> values for the “day” have been expressed as a proportion of 98.4; those for the “night” as a proportion of 1.6. These figures are the percentage ratio of the totals of females caught by “day” to those at “night” in the 3 extended catches, so that the values plotted in Fig. 1 represent percentages of the 24-h total. The figures for males have been calculated in the same way, except that no males were caught at “night”. Fig. 1 shows that the ratio of females to males is more than 6:1.

**DISCUSSION**

The curve of landing activity of females of *A. aegypti*, shown in Fig. 1, presents an almost perfect bimodal symmetry centred about noon. Peak activity occurred most often in the hours during which the sun rose or set, or occasionally up to 1.5 h later in the morning or 3 h earlier in the afternoon. Although the proportion of the peak hours in which the sun was above or below the horizon varied by nearly 0.5 h, it is clear that the shape of the activity curve could not have been altered materially had the times of sunrise and sunset been constant. Every catch was bimodal but few showed symmetry. The number of catches with larger morning peaks equalled the

\[ N \]
\[ i=1 \]

\[ \log_{10}(M_{W} + 1) = \frac{\sum \log_{10}(n_i + 1)}{N} \]

where *n*<sub>i</sub>, *n*<sub>1</sub>,..., *n*<sub>N</sub> represent the actual number of mosquitoes in a series of *N* catches for a given hour.

“Night” is defined here as excluding any hour in which twilight occurs.
Fig. 1. Hourly captures of *Aedes aegypti* landing on man, expressed as the "Williams' Mean" number per h, for the series of catches, adjusted to a percentage of the total for 24 h. The period 05.00–20.00 hours is based on 14 catches, that from 20.00 to 05.00 hours on 3 catches (see text for details). The line with circles represents the data for females; the line with triangles, the data for males. The shaded area indicates the period when the sun was always below the horizon. The narrow columns between the shading and the thin dotted lines indicate the maximum variation in the times of sunrise and sunset.

Table 2. Results of 3 collections of *Aedes aegypti* landing on man (hourly totals from 20.00 to 05.00 or 10.00 hours)

<table>
<thead>
<tr>
<th>Date of catch</th>
<th>Hours (East African Standard Time)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>00 to 01</td>
<td>01 to 02</td>
</tr>
<tr>
<td>24 Apr. a</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>27 May a</td>
<td>2 (0)</td>
<td>2 (0)</td>
</tr>
<tr>
<td>25 June a</td>
<td>0 (0)</td>
<td>1 (0)</td>
</tr>
</tbody>
</table>

| Totals females | 2 (0) | 3 (0) | 5 (0) | 1 (0) | 0 (0) | 0 (0) | 2 (0) | 0 (0) | 38 (1) | 25 (2) | 12 (0) | 7 (0) | 95 (3) |
|               |       |       |       |       |       |       |       |       |       |       |       |       |       |

<table>
<thead>
<tr>
<th>Totals males</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
</table>

a This is a continuation of the catch of the same date recorded in Table 1.
b The figures in parentheses are the totals of males.
	number of catches with larger afternoon peaks and there was no obvious seasonal correlation.

It might be thought that the time of starting the catch could influence the prominence of the morning or evening peaks. The well-developed morning peak in the total catch figures would thus have been the result of starting in the morning, whereas most other studies had later starting times. However, the first hour's catch was always small, and the prominence of the afternoon peak in half of the catches cannot
be denied. Van Someren et al. (1958) started some of their catches at 18.00 hours and some at 12.00 hours, but the prominence of the morning or evening peak was related to the catch site (bush versus house) and not at all to the time of starting (E. C. C. van Someren, personal communication).

Although 13 of the 17 previous series of landing ("biting") catches of A. aegypti have shown a definite bimodality, in none has the morning–afternoon symmetry been as pronounced as in the present study. Symmetry is not uncommon among nocturnal forest mosquitoes, such as several species of Mansonia and Culex, where the peaks often occur during twilight and are sharper and more symmetrical at greater heights above ground level owing to vertical migrations (Haddow, 1961b; Haddow & Ssenkubuge, 1963). Bimodal symmetry has been observed less frequently among diurnally active species. The most obvious example is that of A. irritans (Mattingly, 1949), followed by Hodgesia cytopus and some species of Eretmapodites (Haddow & Ssenkubuge, 1963, 1965). At different heights above ground level, A. ingrami shows periodicities (Haddow, 1961a) very similar to those of several of the A. aegypti series. Within the subgenus Stegomyia, A. apicoargentus shows the sharpest bimodal symmetry in the forest canopy, but its activity is crepuscular (Haddow & Ssenkubuge, 1965); in other studies, it was variable at lower levels (Haddow, 1961b). Rather similar is A. simpsoni, which has at best two rather ill-defined diurnal peaks sometimes tending to merge about three hours before sunset (Lumsden, 1955; Teesdale, 1959; Haddow, 1961a; Gillett, 1969).

Differences in periodicity relative to locality can be very marked, as Haddow (1954) showed with Anopheles implexus, but the all-important question of genetic versus environmental differences remains unanswered. The voluminous literature on the periodicity of "biting", quoted in part above, suggests that both factors can be involved and that the differences between the periodicities of A. aegypti in different series of catches are more real than mere sampling artefacts.

It was therefore impossible to predict anything more than generalized diurnal activity for the population of A. aegypti in Dar es Salaam, and further observations were clearly necessary.

The pale form of A. aegypti was believed by van Someren et al. (1958) to have predominated in their house or house compound series, and the dark form outside. They suggested that this was correlated with the difference in periodicity. The house catches of Teesdale (1955, 1959) are in agreement, but those of McClelland (1960), made in the same village as the catches of van Someren et al. (1958) and also involving the pale form of A. aegypti, showed an unequivocally higher afternoon peak. Lumsden (1957), also working with the pale form, found activity on the verandah higher in the morning; that in the house higher in the afternoon. In none of the catches made by Boorman (1960, 1961) in Nigeria was the morning activity the highest, although the activity inside or near houses was strongly biphasic.

The question of the "colour" forms of A. aegypti, particularly in relation to domesticity, will be discussed more fully elsewhere (G. A. H. McClelland & W. K. Hartberg, unpublished observations). The A. aegypti taken in the present study were from a population that was only slightly paler than the darkest populations in Tanzania (G. A. H. McClelland & W. K. Hartberg, unpublished observations). The automobile dump, though heavily shaded, lacked the undergrowth typical of the bush catch sites of Teesdale (1955) and van Someren et al. (1958) in Kenya. The catches made in the village, houses, or compound by the Kenya workers and those of Lumsden (1957) and McClelland (1960) involved pale forms of A. aegypti and yet show little agreement in detail. There is less of a pronounced dip at noon and more activity at night.

It is perhaps interesting that the periodicity of males recorded by McClelland (1960), Lumsden (1957), and Boorman (1960) in 3 of the 4 series in West Africa, and in the present study, closely agree. Since males do not take a blood meal (which in the case of a female, would probably inhibit host-seeking activity at the time of the next "peak"), they may better demonstrate the underlying, endogenous diphasic rhythm of the species. For example, a greater availability of hosts in the morning might cause a smaller proportion of females to remain unfed and be ready to bite in the afternoon, whereas the males would be unaffected.

Very clear-cut bimodal peaks of sugar-feeding activity were demonstrated in laboratory experiments by Gillett (1961) and Gillett et al. (1962). The phenomenon was shown by both males and females. A. africanus also shows a distinctly bimodal activity curve, although blood-feeding occurs only at the evening peak (Gillett & Haddow, 1957). Morning and evening activity has been recorded at flowers under natural conditions by Larsen (1948) and Haeger (1955).
Differences in host availability might, on the other hand, affect the apparent periodicity of landing on the catching team in a different way, through a dilution effect, although this could be expected to affect males and females similarly. Villagers probably tend to work away from the houses in the mornings but return to rest in or near their houses during the afternoon. In this situation a catching team might include a larger proportion of the available host population in the morning than in the afternoon, resulting in an exaggerated morning peak.

Yet a further possibility needs investigating. Hartberg (1971) found that between 14% and 41% of female A. aegypti taken in “biting” catches near the site of the present study were un inseminated. McClelland & Conway (1971) in the same area found that nearly 18% of the female A. aegypti landing on man would not feed even after a protracted opportunity. Gwadz & Craig (1968) demonstrated that females of A. aegypti cannot be properly inseminated for about the first two days of adult life. Lavoipierre (1958) and Judson (1967) found that un inseminated females fed repeatedly. If the host is the focal point of mating of A. aegypti (Hartberg, 1971) as it is for A. sierrensis (Peyton, 1956; Lee, 1971), a higher rate of host-seeking activity in younger, un inseminated females—matching that of the males—is likely to result in earlier insemination. As A. aegypti breed extensively around the site of the present investigation the proportion of young females may have been high enough to account for the close similarity between the periodicities of the two sexes. In terms of proximity to breeding sites, the house catches made in previous studies resemble the present series more than the bush catches do. A possibly similar effect of proximity of breeding on “biting” periodicity was recorded by Lumsden (1955) in A. pembaensis.

If the detailed temporal pattern of host-seeking or biting in A. aegypti is of some epidemiological significance, answers to the questions raised in this paper should be sought.

ACKNOWLEDGEMENTS

The authors were grateful for the cheerful cooperation of the members of the catching team and for the diligence of their supervisors, G. Mhina, L. Mahikwano, and D. Mkami. This study was supported jointly by US Public Health Service Research Grant No. CC 00261 from the Center for Disease Control, Atlanta, Ga., and by the World Health Organization.

RÉSUMÉ

PÉRIODICITÉ DES CONTACTS ENTRE Aedes aegypti ET L'HOMME AU COURS DU NUCTHÉMÈRE

On a étudié la périodicité des contacts entre Aedes aegypti et l'homme, à intervalles irréguliers pendant un an, dans un habitat du moustique situé dans un faubourg de Dar es-Salaam (Tanzanie). Les moustiques mâles et femelles se posant sur le corps de 3 à 6 hommes ont été capturés par ces derniers et dénombrés chaque heure pendant une période continue de 15 heures ou davantage. 

Au cours d'une séance de capture d'une durée de 28 heures et de deux autres d'une durée de 24 heures, débutant à 6 heures, on a constaté que l'activité nocturne du moustique correspondait à moins de 2% de son activité totale de 24 heures. Onze autres séances, débutant à 5 heures et d'une durée de 15 heures, ont eu lieu. Durant ces 14 expériences, deux clochers d'activité, l'un de 6 heures à 8 heures et l'autre de 15 heures à 19 heures, se sont manifestés. Le nombre des séances caractérisées par un fort clocher matinal était équivalent à celui des séances montrant une activité maximale dans l'après-midi.

Les résultats combinés de l'ensemble des séances de capture font ressortir une nette périodicité diaphasique qui semble une caractéristique relativement peu fréquente de l'activité diurne d'A. aegypti. Les variations de cet aspect du comportement chez différentes espèces de moustiques et différentes populations d'A. aegypti sont évoquées. Sans exclure l'intervention de facteurs génétiques, on estime cependant probable que ces variations sont dues à des facteurs de milieu. L'activité des moustiques mâles, dans différentes études, apparaît plus uniforme que celle des moustiques femelles, car elle n'est pas influencée par la nécessité des repas de sang, et elle rend mieux compte du rythme endogène propre à l'espèce.
REFERENCES

Gillett, J. D. (1961) Nature (Lond.), 190, 881
Gillett, J. D. et al. (1962) Ent. exp. appl., 5, 223
Haeger, J. S. (1955) Mosquito News, 15, 21
Trpis, M. (1962) Biologia (Bratislava), 17, 123