

## Diurnal periodicity of flight by insects

By T. LEWIS AND L. R. TAYLOR

*Department of Entomology, Rothamsted Experimental Station, Harpenden, Herts.*

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### SYNOPSIS

An account is given of the diurnal flight periodicity of 400 taxa, based on data obtained from about half a million species collected in suction traps in various localities, mainly in southern England. The effect of light intensity and the relation of size and colour to the time of flight are discussed. The evolution of night flight in certain orders is considered.

### I. INTRODUCTION

INSECT flight is periodic. With rare exceptions, insect species fly during only part of the 24 hours, and we use the term diurnal to describe periodicity involving a 24-hour cycle. Time of flight is determined largely by physiological responses to cyclic factors in the environment. Light intensity is usually the factor that affects the time of flight, whereas temperature influences amplitude. These factors may act by initiating flight in a resident population or by initiating emergence of alate adults.

The published analyses of flight periodicity are scanty, and some are unreliable, having been collected by inadequate techniques. We therefore present evidence of the flight periodicities of about 400 insect taxa, represented by about half a million individuals sorted from a total of 5 million insects collected at 46 sites, some from every month of the year. Some basic principles emerge that relate time of flight to colour, habitat and migration, but formal analysis of causal factors is not attempted. Our first purpose is to catalogue the flight periodicity of at least some representative insect groups, in order to make discussion and subsequent analysis of individual response curves possible and to provide a background for work on migration and for any other study involving sampling or observation of flying insects.

### II. SAMPLING METHODS AND ANALYSIS

#### *The Trap*

Insects were collected continuously by 9-inch Ventaxia or 12-inch Aerofoil suction traps (Johnson, 1950a; Taylor, 1962), which separated the catch into 30-, 60- or 120-minute samples. The inlet of the traps was sometimes modified by flexible tubing to reach inaccessible habitats. The collections were, we think, unbiased by the presence

of the trap. All times are G.M.T. unless stated otherwise. Most of the records are new, but we have also included some already published records of collections made by suction trap or other unbiased method, for completeness. We also refer in discussion to periodicities described from visual observation where these are relevant. We have excluded references to periodicities obtained by attractant traps, particularly light traps, which have repeatedly been shown to be strongly biased by the behaviour of the insects towards the trap itself (Williams, Singh & el Ziady, 1956; Provost, 1959; Taylor & Carter, 1961).

#### *The Sites*

The sites were selected to cover as wide a range of habitats as possible. Aquatic habitats were represented by a river, a stream, a lake and a small pond, and semi-aquatic habitats, in which decaying organic matter predominated, by sewage filter beds and mushroom beds, rotting compost, wet moorland, ditches and a salt marsh. Catches were also made in many agricultural crops including pasture, oats, wheat, beans, kale, potatoes and pyrethrum, and on waste ground among nettles, willowherb and comfrey. Other traps were in orchards, among gorse and broom on a dry heath, in new woodland containing *Euonymus*, *Rhododendron*, beech, elm, pine and oak, and in an ancient birch, beech and oak woodland. The sites and their vegetation are listed in *Appendix A*.

#### *The Catch*

Each point shown in the figures represents a sample mean, usually derived from catches of 5–14 days duration, so that minor fluctuations caused by weather or small numbers are smoothed out as far as possible. The resultant series of 12, 24, or 48 samples per day is considered to represent, more or less closely, the basic diurnal periodicity of numbers in flight per unit volume of air (aerial density) at the named site. Periodicity curves for a given species from different sites were usually similar.

Only occasionally have we attempted to relate this periodicity to environmental factors, although the effect of changing time of sunset and the limiting action of light and temperature thresholds are illustrated.

#### *The Fitted Curves*

Because there are over 400 periodicity curves to describe, it was necessary to tabulate results. To do this succinctly, we have fitted probability distributions to the observed time sequences of samples and the curve drawn through the points is transformed from this.

It must be emphasised that we imply no theoretical significance by these distributions, which are an empirical convenience only. The curves drawn in the figures are also only our provisional interpretation of the data, susceptible to correction or revision as material improves; in particular, we use the word "normal" merely to mean "not skew". Many species have two periods of flight within each 24 hours, and these two peaks of activity are as evident when plotted on probability paper as in the original data. Until it has been shown that the insects in flight during one peak of activity are the same individuals as those in the other, we cannot assume that both distributions describe the same population. For example, individuals of *Doralis fabae* (Aphididae) in flight during the morning differ from those flying during the afternoon. The former have waited overnight for light and temperature to exceed the flight threshold before taking off, whereas the afternoon flyers have taken off as soon as they are flight-mature (Johnson & Taylor, 1957). Again, the morning peak for *Lithocolletis messaniella* (Lepidoptera) consists largely of males, and the evening peak of females (Crichton, *personal communication*). Also, the peak of *Neuroterus quercusbaccarum* before dawn is largely composed of males, and the afternoon peak of agamic females.

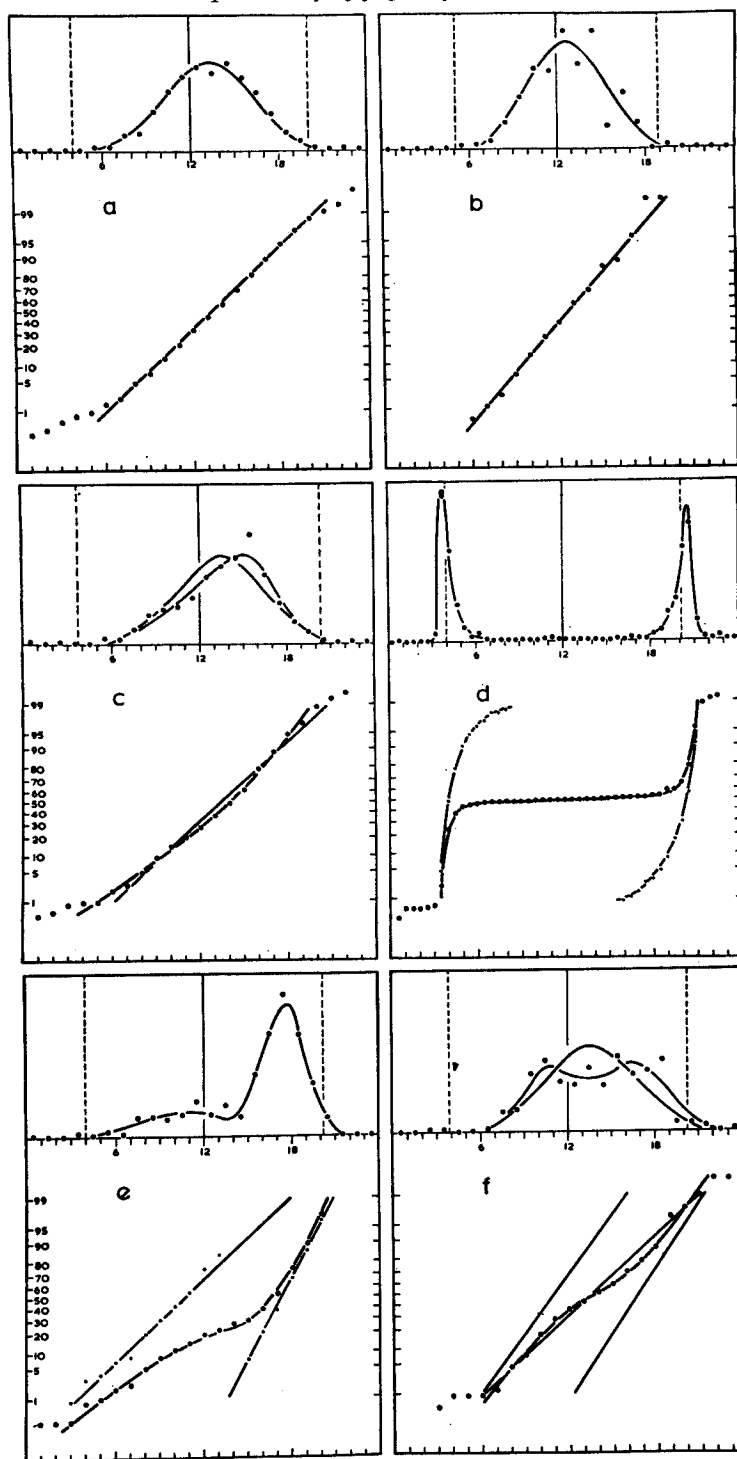


FIG. 1.—Fitting probability curves to flight periodicity samples. (a) *Oscinella frit* (Chloropidae), females, July 1960; (b) *Bombus agrorum* (Apidae), August 1963; (c) *Oscinella frit*, males, June 1960; (d) *Drosophilidae*, July 1952; (e) *Cavariella aegopodii* (Aphididae), July 1949; (f) *Phaonia rufipalpis* (Muscidae), June/July 1962. The flight periodicity curve drawn above is derived from the line drawn through the accumulative percentages below. In double distributions (d, e, f) this is compounded from the two single distributions given in the lower part of the figures.

It is occasionally difficult to decide whether to describe a flight periodicity curve as uni-, bi- or multimodal. Failing better criteria, we have used our judgment, considering the appearance of the periodicity curve on a time scale and on the probability plot, and also any biological factor known to us. In practice the category is usually self-evident, and either one or two lines can be drawn on the probability plot, using the method of Harding (1949) to separate the bimodal ones. When there are two, the resulting distributions are considered provisionally to derive from separate populations.

Figure 1 illustrates the kind of results obtained by this method. The first curve (fig. 1, *a*), for females of *Oscinella frit* (Diptera), July 1960, is an almost perfect single distribution. The tails at either end are artifacts caused by deficiencies in the segregating mechanism of the trap, and account for the 2 per cent. of the total catch that gets into the wrong sample.

The second curve (fig. 1, *b*), for males of *Bombus agrorum* (Hymenoptera), August 1963, is included to show how much scatter in the points for the periodicity curve is tolerable in fitting the probability curve. The considerable scatter in the hourly catches during the afternoon barely affects the linearity of the probability plot and there is no reasonable doubt about how to draw it.

The third curve (fig. 1, *c*), for males of *Oscinella frit* (Diptera), June 1960, is apparently a single distribution, whose skewness could be rectified by transforming the time co-ordinate. This was not done for two reasons. First, the skewness is not consistent from month to month, or constant between sexes, and we think it is fortuitous. Second, the prime object of fitting curves is to obtain a simple, convenient description of the data suitable for tabulation as arithmetic means and standard deviations. The inconvenience of asymmetrical positive and negative standard deviations, resulting from detransforming fitted skew curves, would outweigh any doubtful gain from a perfectly fitting skew curve. The symmetrical curve is therefore the one tabulated. However, we have recorded skewness and its direction with reference to the time of maximum light (*Appendix B*) so that consistency, within a taxon or otherwise, may be noted in the general discussion of results.

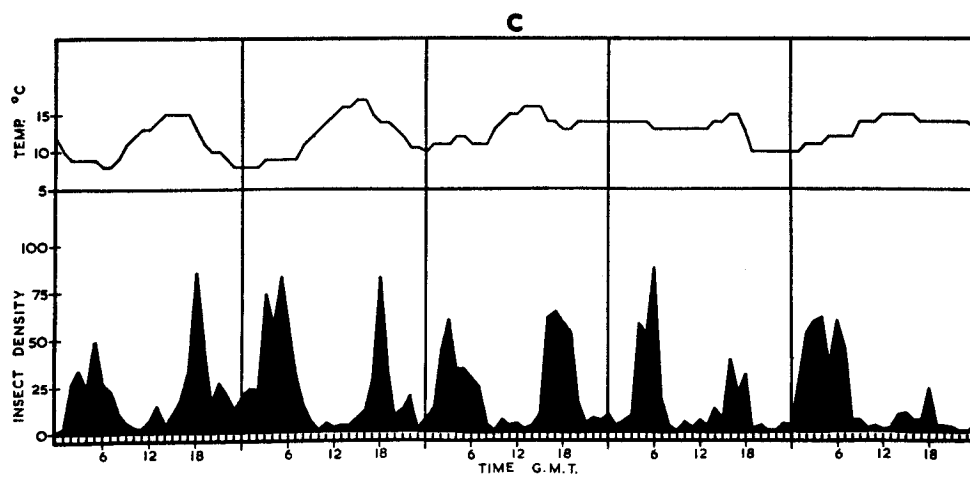
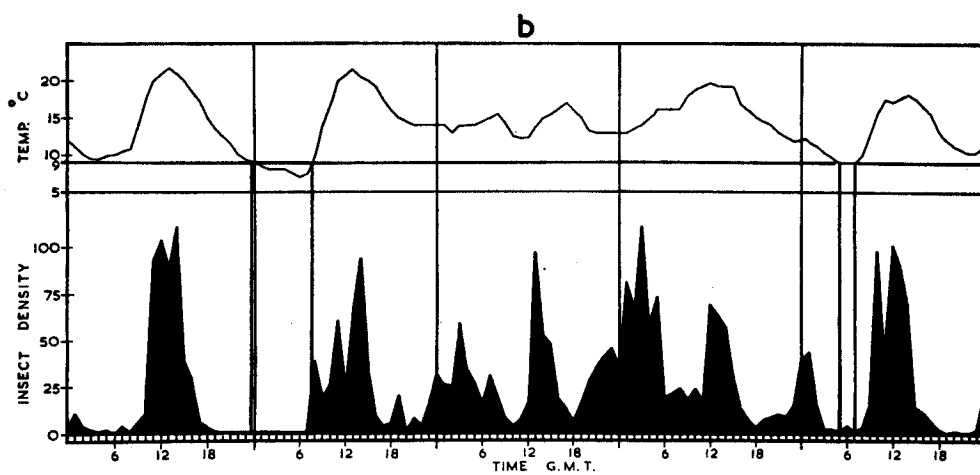
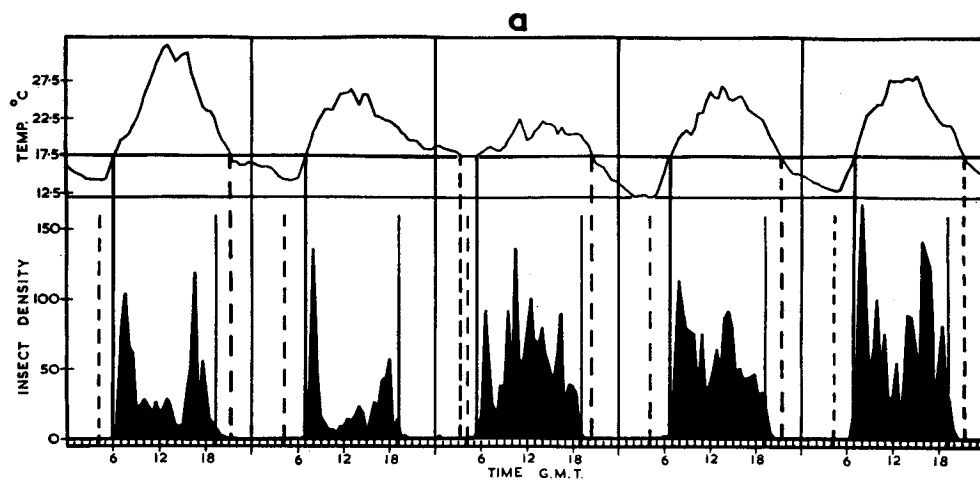
The fourth curve (fig. 1, *d*), *Drosophilidae* (Diptera), July 1952, is the simplest example of bimodal distribution, 50 per cent. at dawn and 50 per cent. at dusk. In addition to the sigmoid probability curve for the whole 24 hours, we have plotted the two expanded individual distributions. These remain skewed after separation. The population is a mixture of three species from three different genera and results in an almost perfectly regular double distribution. Nevertheless, fewer of both sexes of two species flew at dawn than at dusk, whereas in the third species fewer males flew at dusk, but females flew equally at dawn and dusk. A regular sample distribution does not mean that the parent population is uniform.

The fifth curve (fig. 1, *e*), for *Cavariella aegopodii* (Hemiptera), July 1949, is a typical example of paired distributions, erratic in timing relative to the sun and unequal in size, that are to be expected with insects like aphids, a measurable proportion of the flying population of which is formed by the current day's production of newly flight-mature individuals. These two distributions are easily separated and probably come from different populations. They are treated as bimodal distributions in the table.

The sixth curve (fig. 1, *f*), for *Phaonia rufipalpis* (Diptera), June/July 1962, shows the

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FIG. 2.—Light and temperature thresholds. (*a*) *Doralis fabae* (Aphididae). The temperature threshold (17.5° C.) usually operates in the morning and the light threshold (19.15 hours) operates in the evening. (*b*) *Aleyrodes proletella* (Aleyrodidae). There appears to be no light threshold in this autumn generation. When the temperature threshold is exceeded, the peaks of flight occur erratically, dependent upon rates of ecdysis. (*c*) *Lithocolletis messaniella* (Gracillariidae). There are two peaks of flight, one composed mainly of males in the early morning and another mainly of females in the evening, the timing being fairly stable. "Insect density" refers to numbers trapped per 20,000 cu.ft. of air.



most difficult problem. The fitted sigmoid probability curve separates into the two distributions shown in the figure, each comprising 50 per cent. of the total distribution with means at 11.00 and 17.00 hours, and both with standard deviations of 2 hours. Nevertheless, we have tabled the data as a single distribution with a mean at 13.38 hours, for we have no reason to suppose that the insects caught in the morning differ from those caught in the afternoon. The flying life of these large Muscidae is probably several weeks, and many caught in the trap were old and worn. The local population probably does not vary greatly from day to day and certainly not from hour to hour. Hence the same insects probably fly intermittently throughout the day when light and temperature permit. Provided the weather remains fairly constant, so that light and temperature thresholds inhibit flight at about the same time each day, we expect the mean flight curve to be flat-topped. When the weather is less constant, and the time of operation of thresholds varies, the curve becomes more normal. There is no reason why the two peaks of activity should separate. From what is known of the biology, we assume that the flat-topped form here is incipiently unimodal, not bimodal; this is a borderline example.

#### *Flight Thresholds*

Figure 2 illustrates the operation of light and temperature thresholds. A temperature threshold of  $17.5^{\circ}\text{C}$ . must be attained each morning before *Doralis fabae* (fig. 2, a) can begin to fly, but flight is inhibited by failing light at 19.15 hours each evening, while temperatures are still above  $17.5^{\circ}\text{C}$ . (Taylor, 1963). During the daytime, peaks can occur at all times and many curves are bimodal (Johnson, Taylor & Haine, 1957).

The temperature rarely falls below the flight threshold of  $9.0^{\circ}\text{C}$ . for *Aleyrodes proletella* (fig. 2, b), and darkness does not inhibit flight, which continues through the night. The timing of peaks is erratic, and is dependent on the numbers that become flight-mature, not on current weather (El Khidir, 1963). Temperature thresholds for flight have also been demonstrated in *Oscinella* (Smith, 1962), *Limothrips* (Lewis, 1963) and *Agrochola*, *Amphipyra*, *Rhagonycha* and *Vespula* (Taylor, 1963).

Neither light nor temperature inhibited flight of *Lithocolletis messaniella* (fig. 2, c), which flew at all hours, the males mainly in the early morning and the females in the afternoon; the causes of the peaks are not yet known (Crichton, *personal communication*).

#### *Classification of Flight Periodicity*

We have classified all the periodicities according to the following criteria. *Single distributions*: wide or narrow, *i.e.* with standard deviations greater than or less than  $\pm 90$  minutes; normal or skew towards light (*i.e.* the mode is nearer to noon than is the mean) or skew away from light; mean activity at dawn, morning, noon, afternoon, dusk or night. *Double distributions*: mean times of flight equally spaced about noon or unequally; peaks equal in size, or greater before or after noon; normal or skew towards light, or skew away from light; the two peaks separate or overlapping, *i.e.* distance between the means more or less than the sum of the two standard deviations. Two distributions had more than two peaks and were classified as indeterminate. Of the resultant 73 possible categories, only 42 examples were found in our material. We have illustrated these 42 with small sketches (fig. 18, p. 468) and each species is referred to one of these (see also *Appendix B*). Indeterminate curves (type 43) are not illustrated. It seems likely that at least some of the remaining 31 categories will eventually be found as material accrues.

For convenience, insects have sometimes been classified arbitrarily as either "day" or "night" flyers (*see* Tables V and VI). The criterion adopted for "daylight" is mean time of flight at light intensity greater than 1000 f.c. This occurs approximately one hour before sunset and one hour after sunrise. Hence crepuscular insects are classified with "night" flyers for this purpose.

## III. EMERGENCE AND THE TIME OF FLIGHT

There is a large literature on diurnal periodicity of emergence from the pupa in many orders (Bremer, 1926; Harker, 1958; Mell, 1939; Morgan & Waddell, 1961; Nielsen & Haeger, 1954; Palmén, 1955; Pittendrigh, 1954; Remmert, 1955, *a* & *b*), but the relationship between emergence of the adult and time of flight is rarely discussed.

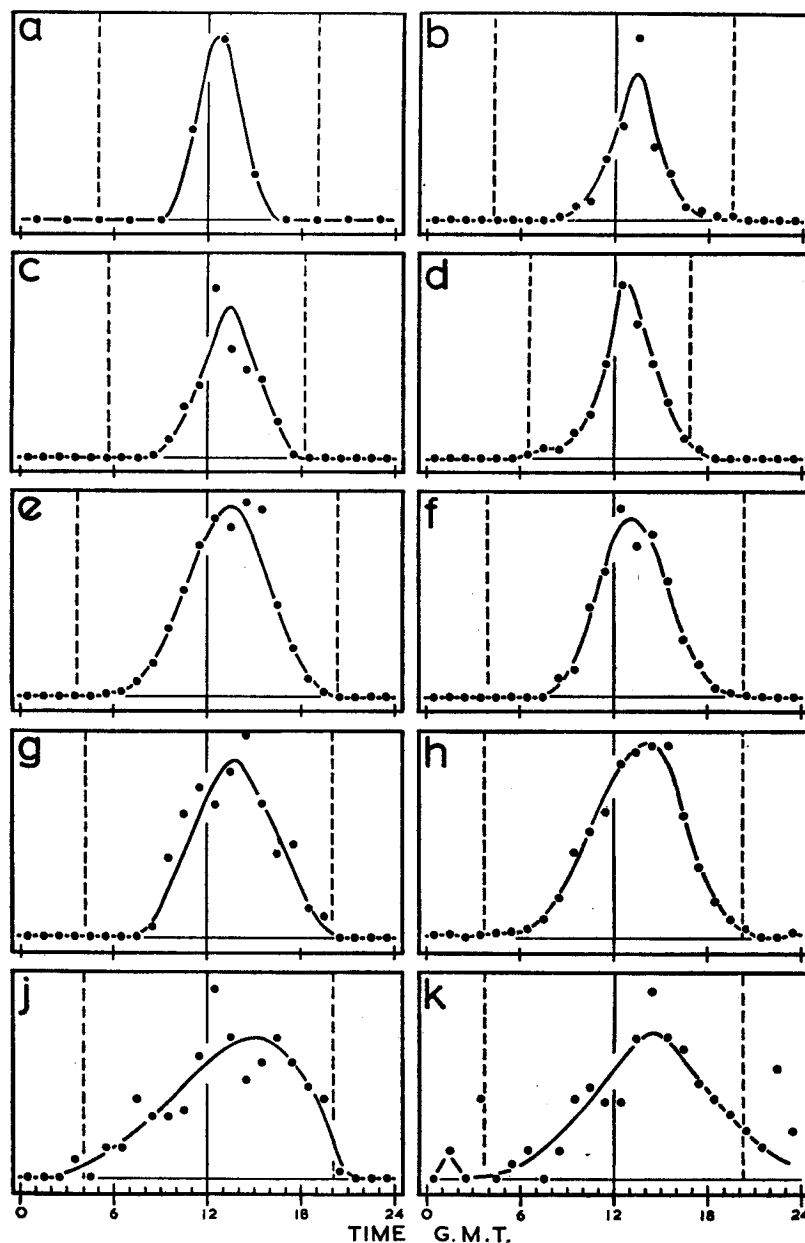


FIG. 3.—The duration of the daily flight period. (a) *Nymphalis io* (Nymphalidae : Lep.); (b) *Hylemya* sp. s.s. (Muscidae : Dipt.); (c) *Apis mellifera* (Apidae : Hym.); (d) *Apanteles circumscriptus* (Braconidae : Hym.); (e) *Limothrips cerealeum* (Thripidae : Thysanop.); (f) *Dolichopus unguatus* (Dolichopodidae : Dipt.); (g) Mixed Chalcidoidea (Hym.); (h) *Oscinella frit*, females (Chloropidae : Dipt.); (j) *Phyllostromia melanocephala* (Empididae : Dipt.); (k) *Phyllobius argentatus* (Curculionidae : Col.).

In most long-lived species, the pattern of the curve showing daily flight periodicity may not be directly influenced by the initial emergence rhythms of the adult. Females of many species, e.g. *Culex pipiens* and *Syrphid pipiens*, exhibited the same flight periodicity whether they were old and gravid or newly-emerged. The Syrphid *Microdon* sp. emerges from the pupa at night (Park, 1940), but from our evidence Syrphids appear to be exclusively day-flyers (fig. 17).

The pattern of flight periodicity among old individuals of other species may be reinforced by an emergence rhythm. For instance, *Scopeuma stercorarium* has a pronounced emergence rhythm that reaches a peak between 09.00 and 14.00 hours each day, and few flies emerge during the night (Lewis & Bletchley, 1943). Numbers of this species in flight also reached a peak about 13.00 hours and, when the teneral period is short, the daily emergence rhythm may intensify this peak. Nevertheless, the contribution of the emergence rhythm could only be small because old flies, which are usually most abundant, also fly most at 13.00 hours. In Odonata (Corbet, 1962; Morgan & Waddell, 1961), emergence rhythms may also reinforce the pattern of the flight periodicity curve.

The emergence rhythm of very short-lived species is probably the dominant factor influencing the time of flight in suitable weather. Ephemeroptera, especially those stream dwellers that fly in the evening, emerge and fly within a very short period (Sprules, 1947). Of the Trichoptera, both lake-dwelling (Morgan & Waddell, 1961; Scott & Opdyke, 1941) and stream-dwelling forms (Sprules, 1947) emerge between dusk and midnight, and most are crepuscular flyers. Morgan (1956) found *Athripsodes aterrimus* emerging and flying during daylight and at Oakfield *Orthotrichia tetensii* had two peaks of flight, one at 10.00 hours (fig. 15, d). The time of flight of many Chironomidae is also probably closely associated with emergence (Morgan & Waddell, 1961; Palmén, 1955). There are varietal differences between individuals of the Chironomid *Microtendipes chloris* Meigen that emerge at midday in March and April and those that emerge in darkness in June and July (Morgan & Waddell, 1961). These authors also suggest that the presence of two forms of *Chironomus pulsus* Walk. accounts for the different times of emergence in different seasons. However, the change in time of emergence of many Chironomids matches the seasonal change in the time of sunset, the time being governed by the change from light to darkness (Palmén, 1958; Sprules, 1947). Conversely, in *Drosophila* (Brett, 1955; Pittendrigh, 1954) and in the Chironomid *Pseudosmittia arenaria* Strenzke (Remmert, 1955), the final synchronisation of the time of emergence is achieved by the change from darkness to light.

The rapidity with which flight succeeds emergence will depend mainly on the length of the temperature-dependent teneral period (Taylor, 1957) and weather (Lewis, 1963; Taylor, 1963). Until the length of the teneral period of individual species is known, relationships between rhythms of emergence and flight will remain speculative; our curves do not imply any such relationship.

#### IV. DURATION OF THE DAILY FLIGHT PERIOD

Figure 3 illustrates a series of flight curves, all with maximum activity near noon but with progressively longer periods of flight. *Nymphalis io* (fig. 3, a) and *Hylemya* sp. (fig. 3, b), with standard deviations of 75 and 96 minutes, respectively, flew mainly during three hours in the middle of the day. This contrasts with *Phyllochromia melanocephala* (S.D. 231) (fig. 3, j) and *Phyllobius argentatus* (S.D. 318) (fig. 3, k), which flew throughout the day and intermittently during the night. Honey bees, parasitic Hymenoptera, thrips, some Dolichopodids and frit flies (fig. 3, c-h) had standard deviations between these two extremes.

For day-flyers, the duration of suitable light intensity limits the period when flight is possible. The examples shown in figure 3 are mainly from summer catches, so that, if light is the limiting factor, the short-period flyers must be responding either to very



high light intensities or, in shaded places, to relatively strong light. From the shape of the light intensity curves (fig. 4), which are flat-topped (indicating that light changes little from 08.00 to 16.00 hours in June), this seems improbable. However, direct sunlight is essential for flight in some insects, and this may be the explanation of the short period of flight. We do not know what other factors might limit flight to such a short period at midday. The duration of flight in day-flyers was often clearly related

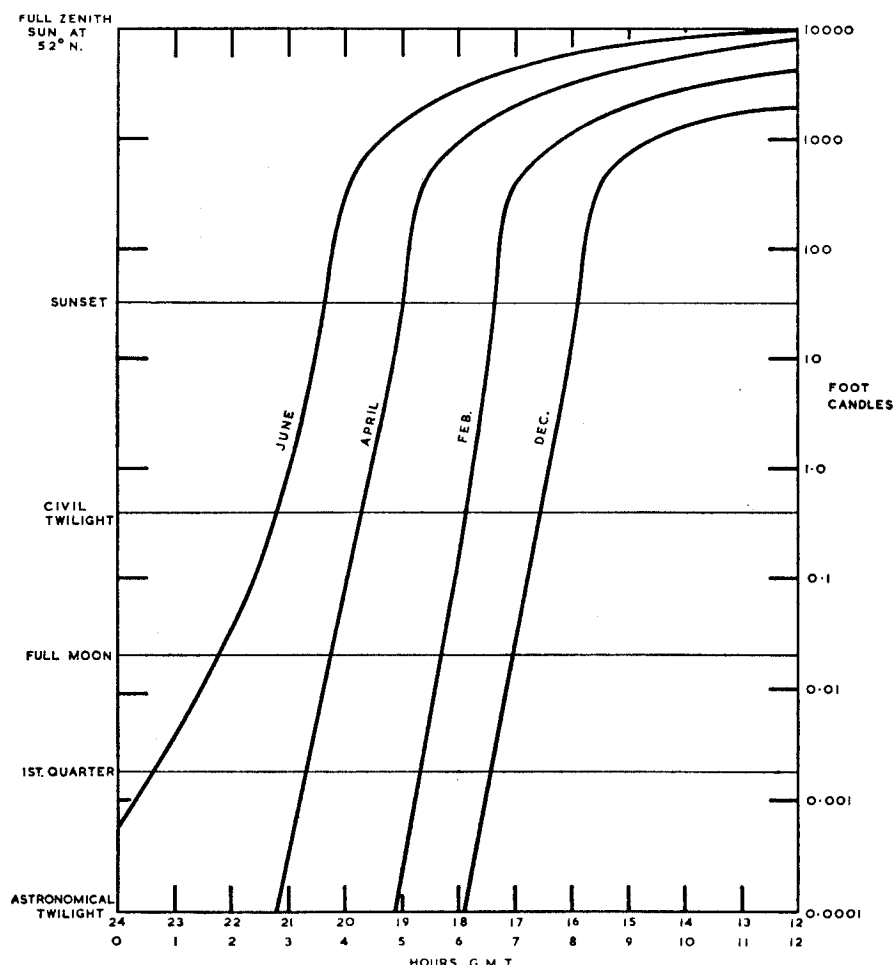


FIG. 4.—The diurnal cycle of log. light intensity at 52° N. with a clear sky in the months of December, February, April and June. The other months are distributed fairly evenly between these. On this log. scale, which is the best approximation to the visual response of animals, light changes rapidly from starlight to sunrise, but much more slowly once the sun is up. Cloud cover may reduce these values considerably, especially in winter-time.

to specific kinds of behaviour. Many Empididae and Rhagionidae, and some Dolichopodidae, which hunt on the wing, flew characteristically for a longer time each day than did the flower-feeding species. Some Empididae fly even at midnight (Morgan & Waddell, 1961).

#### V. SEX AND THE TIME OF FLIGHT

Both sexes of most species fly together, as do those of *A. proletella* (fig. 5, j, k), but this is not always so. During some months the numbers of males of *Oscinella frit* in the air reach a maximum slightly later in the day than do those of the females, but

usually there is no difference (French, *personal communication*). Both sexes of Syrphids usually reached maximum numbers about midday, but only males of *Metasyrphus consisto* were caught, most of these being taken at 09.10 hours (fig. 17, *l*). This was exceptionally early for the Syrphidae, and perhaps females of this species are active at noon, as are the females of closely related species.

Larger and more consistent differences between the sexes occurred in *Drosophila subobscura*; both sexes respond to the same light intensities, but males predominated at dawn and females at dusk, perhaps because males have a lower temperature threshold for flight (fig. 5, *c, d*). In contrast, both sexes of *Drosophila disticha* (fig. 5, *e, f*) and of *Culex pipiens* (fig. 5, *g, h*) flew at the same time, and flight curves of gravid and non-gravid females of *Culex pipiens* were the same.

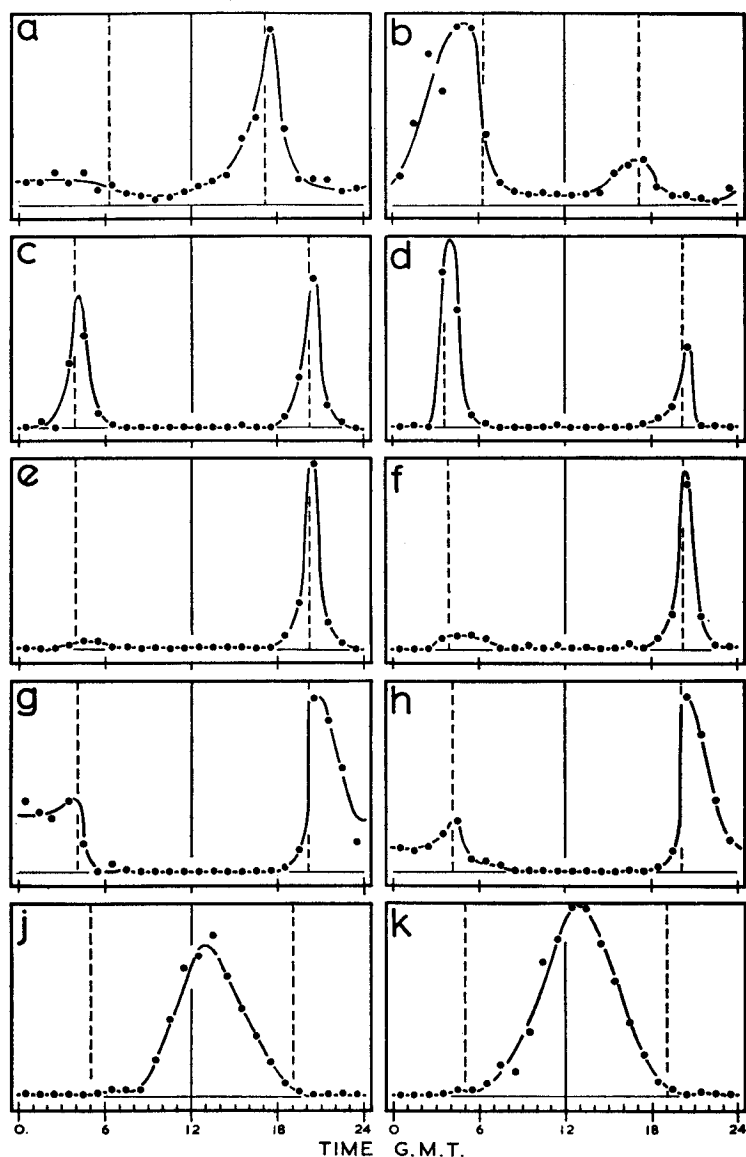


FIG. 5.—Periodicity curves for different sexes. *Lithocolletis messaniella* (Gracillariidae: Lep.): (a) females; (b) males. *Drosophila subobscura* (Drosophilidae: Dipt.): (c) females; (d) males. *Drosophila disticha* (Drosophilidae: Dipt.): (e) females; (f) males. *Culex pipiens* (Culicidae: Dipt.): (g) females; (h) males. *Aleyrodes proletella* (Aleyrodidae: Hem.): (i) females; (j) males.

The most puzzling differences between the flight times of different sexes occurred with the moth *Lithocolletis messaniella*. A few specimens of both sexes were caught throughout the 24 hours, but the periodicity curve was distinctly bimodal, males predominating in an early morning peak and females in a peak at sunset (fig. 5, a, b). Edwards (1962) found differences in the periodicity curves of different sexes of some moths (see p. 425). Females of *Anagasta kuhniella* flew most at sunset, but males flew most at sunrise. A similar curve to the one for *L. messaniella* occurred with the Cyni-

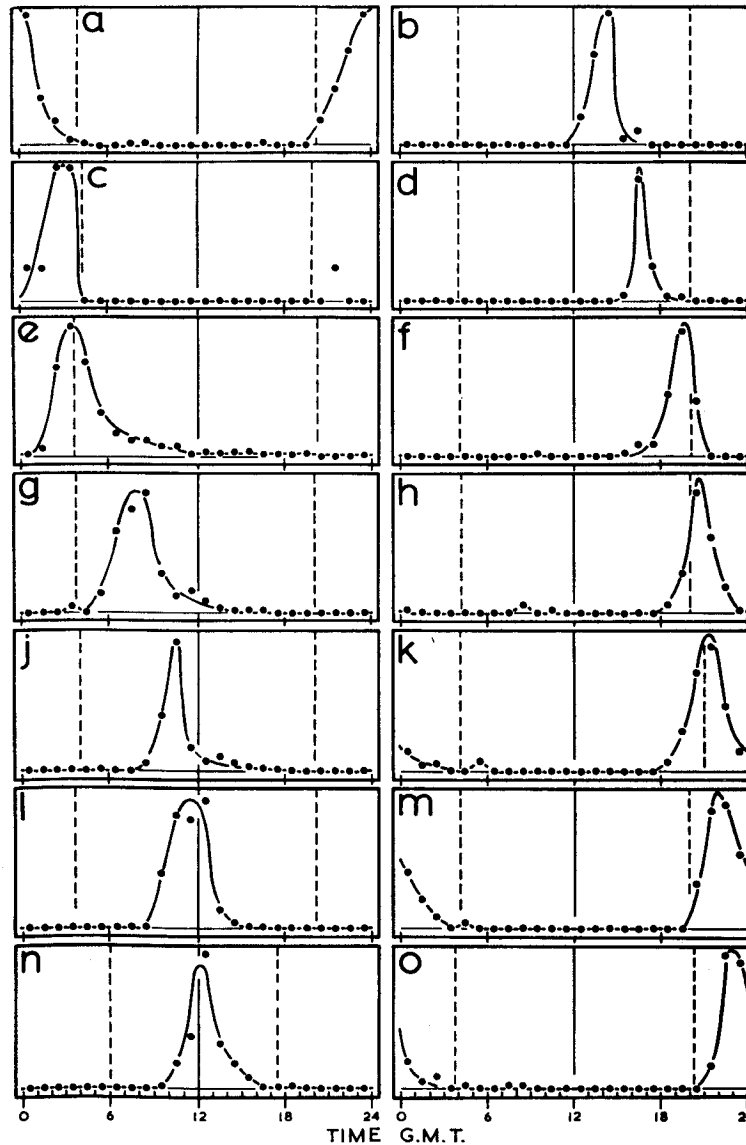


FIG. 6.—Periodicity curves illustrating flight of various insects at all times of the day and night. (a) *Crambus perlellus* (Crambidae: Lep.); (b) *Oligota* sp. (Staphylinidae: Col.); (c) *Celaena secalis* (Caradrinidae: Lep.); (d) *Oxytelus tetracaratus* (Staphylinidae: Col.); (e) *Neuroterus quercus-baccarum*, males (Cynipidae: Hym.); (f) *Atomaria pusilla, lewisi, fuscata* (Cryptophagidae: Col.); (g) *Amauronematus amplus* (Tenthredinidae: Hym.); (h) *Eucosma cana* (Eucosmidae: Lep.); (j) mixed *Lestremiinae* (Cecidomyiidae: Dipt.); (k) *Platyptilia pallidactyla* (Alucitidae: Lep.); (l) *Dilophus febrilis* (Bibionidae: Dipt.); (m) *Hypena proboscidalis* (Plusiidae: Lep.); (n) *Phyllotreta consobrina* (Chrysomelidae: Col.); (o) *Tortrix costana* (Tortricidae: Lep.).

pid *Neuroterus quercusbaccarum*, in which there was a peak before dawn and another in the early afternoon (fig. 15, j); the dawn peak consisted entirely of males of the sexual generation (fig. 6, e), and the daytime peak of agamic females only. No explanation for these sexual differences in flight times in these species is known; with *N. quercusbaccarum* it is not merely a local effect, as it occurred at both Oakfield and Rothamsted.

## VI. RESPONSE TO LIGHT AND FLIGHT PERIODICITY

### Light and Flight

Figure 6 shows that one species or another is in flight at all times, from midday in bright sunlight to midnight in starlight. Figure 4 shows that these times correspond

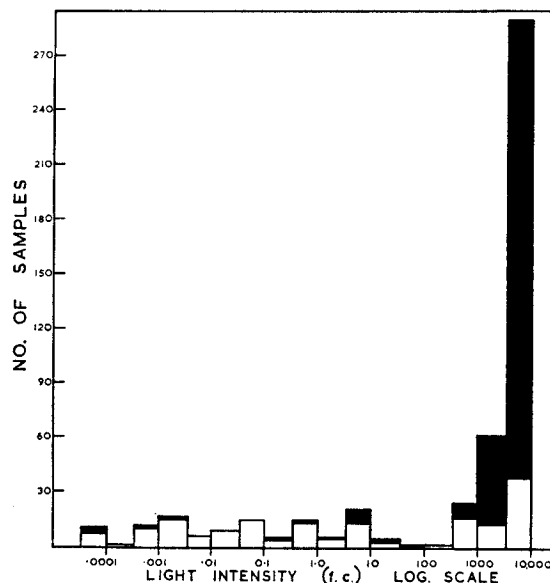


FIG. 7.—The distribution of the mean times of flight in relation to light intensity. Nematocera, Trichoptera and Lepidoptera fly at all light intensities (unshaded areas) but the other insect species (shaded area) fly mainly in bright sunlight.

to a range of light intensities from  $10^4$  to  $10^{-4}$  foot candles. The light at the mean time of flight of each species has been estimated from these curves and has been given in *Appendix B*, and the frequency distribution is shown in figure 7.

Although there is a preponderance of insects flying in bright light, many still fly in near darkness. Visual acuity of these night-flying insects must be fully efficient to permit flight at these times, but there are few analyses of visual acuity in relation to light intensity to verify this.

The only two full response curves seem to be those by Hecht and his colleagues (Hecht, 1928; Hecht & Wald, 1934; Hecht & Wolf, 1929) for *Drosophila melanogaster* and for *Apis mellifera*, two insects with different responses to light that illustrate the adaptive relation of insect vision and time of flight (fig. 8). Near maximum visual acuity is reached at a lower light intensity by the bee than by man, *i.e.* in light rather brighter than at sunrise or sunset. However, man can see to work out of doors in light as dim as Civil Twilight, 0.4 f.c., with about 50 per cent. visual acuity, but visual acuity in the bee is reduced to 50 per cent. before light fades to Civil Twilight, *i.e.* when it is about 1.4 f.c. Our records show that bees rarely continue to fly so late, probably because cold inhibits them, but the flights of *Vespula rufa* continue almost from sunrise to sunset, with a flat-topped distribution suggesting that its flight was usually stopped

by light thresholds both at dawn and at dusk. The light threshold for *Doralis fabae* (Taylor, 1963), another day-flying species, has been demonstrated from field data by plotting the percentage frequency of flight occurrences at half-hourly intervals.

Unlike man and the bee, *Drosophila melanogaster* has 100 per cent. visual acuity in light less than that at sunset and 50 per cent. acuity at 0.04 f.c., nearly as dim as full zenith moonlight. We have no flight curve for this species, but the three species of Drosophilidae we caught in July, *Drosophila disticha*, *Drosophila graminum* and *Drosophila subobscura*, all have the bimodal dawn and dusk flight typical of so many species of Drosophilidae, e.g. *D. melanogaster*, *D. funebris*, *D. obscura* (N.W. & E.A.

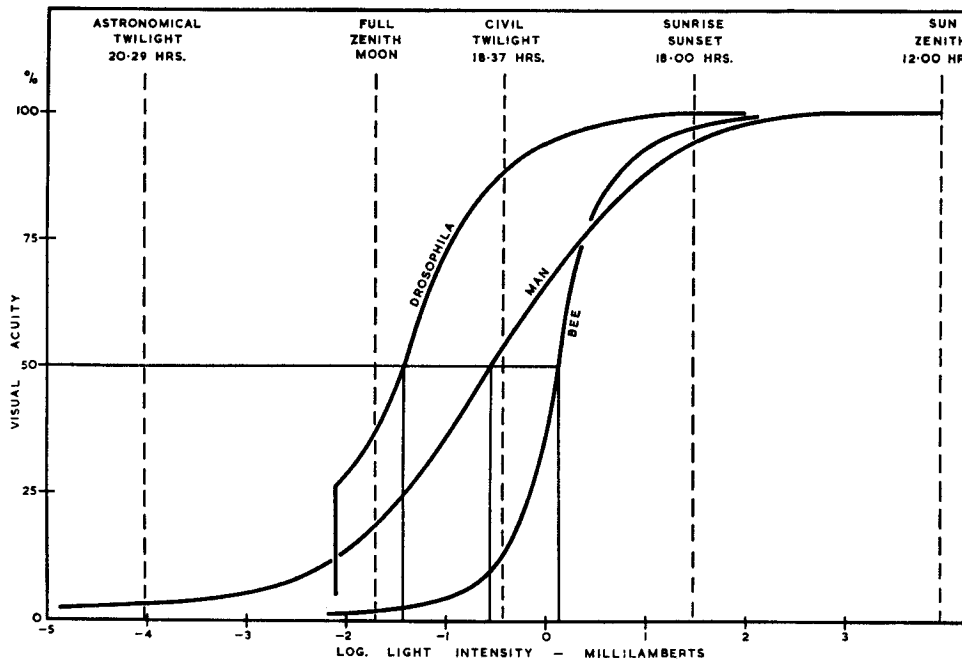


FIG. 8.—Relative efficiency of visual acuity in relation to light and time in man, *Apis* and *Drosophila*.

Timofeeff-Ressovsky, 1940); *D. subobscura*, *D. simulans* and *D. hydei* (Dobzhansky & Epling, 1944); *D. medio*, *D. capricornis*, *D. willistoni*, *D. griseolineata*, *D. bocaniensis*, *D. guarani*, *D. bandieratum* and *D. calloptera* (Pavan, Dobzhansky & Burla, 1950). These last authors point out that the bimodality disappears in rain forests "at least on cloudy days", and Dyson-Hudson (1956) showed clear bimodal periodicity of feeding flight for *D. subobscura* in meadows and open woodland but not for *D. obscura* in dense woodland, although the light intensities at maximum feeding flight were between 2 and 20 candles per ft.<sup>2</sup> = 0.6 to 6.0 equivalent foot candles for both species. *D. pseudoobscura* flies between 15 and 100 f.c. (Mitchell & Epling, 1951). In our samples, the mean flight times for males and females of all species of Drosophilids in July occur at an estimated light intensity of 3–4 f.c.; the estimated light values for October are probably much too high because no allowance is made for cloud. Taylor & Kalmus (1954) showed how the flight time of *D. subobscura* moved with time of sunset (see fig. 9).

Taylor (1963) found no upper light threshold for flight by *Doralis fabae*; nor did Hecht and his colleagues find that visual efficiency of *Apis mellifera* or *Drosophila melanogaster* declined at all at greater light intensities. Flight in *Drosophila* may be initiated at some lower light threshold, related perhaps to the curve for optical efficiency shown in figure 8, but we have no indication whatever why flight should be inhibited

when light exceeds 100 f.c. Reuben (1963) demonstrated an upper light threshold at 22.7 cal./cm<sup>2</sup>/hr. for *Culicoides impunctatus*.

It is evident that the greater visual efficiency in dim light of *Drosophila* compared with that of *Apis* is an ecological adaptation to enable flight at dawn and dusk, but whether or not it is to avoid desiccation, as suggested by Mitchell & Epling (1951), Taylor & Kalmus (1954) and others, is more questionable. Old, desiccated and antenna-less individuals of *D. melanogaster* all prefer higher humidities (Pertunnen & Syrjamäki, 1958), but flies younger than two weeks prefer moderate humidities to high ones (Pertunnen & Ahonen, 1956; Pertunnen & Salmi, 1956), and humidity is not a factor governing their flight in nature (Mitchell & Epling, 1951). We suggest that the dawn and dusk flight of Drosophilidae is adapted to their feeding habits, as with many other evening flyers (see p. 408), rather than to their susceptibility to desiccation.

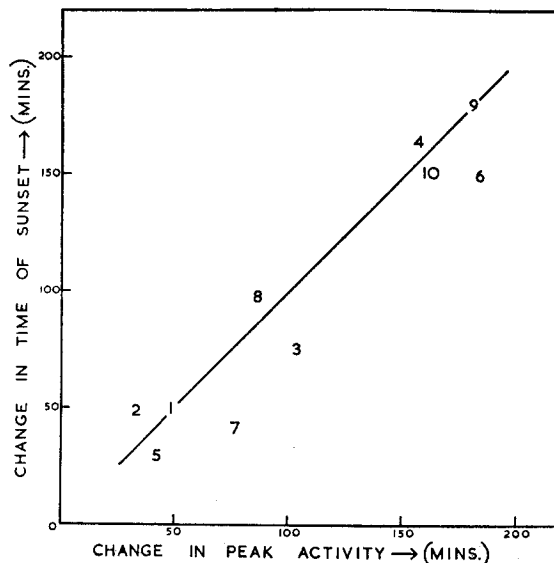


FIG. 9.—Changes in the time of peak activity related to changes in the time of sunset. (1) *Crambus culmellus* (Crambidae: Lep.); (2) *Plutella maculipennis* (Plutellidae: Lep.); (3) *Atomaria lewisi* (Cryptophagidae: Col.); (4) *Limonia nubeculosa* (Tipulidae: Dipt.); (5) *Trichocera annulata* (Trichoceridae: Dipt.); (6) *Tanytarsus atrofasciatus* (Chironomidae: Dipt.); (7) *Culicoides obsoletus* (Ceratopogonidae: Dipt.); (8) *Mycetophila fungorum* (Mycetophilidae: Dipt.); (9) *Mycetophila ocellus* (Mycetophilidae: Dipt.); (10) *Drosophila subobscura* (Drosophilidae: Dipt.).

### Seasonal Changes

For the crepuscular-flying species especially, changes in the time at which most individuals are caught are closely related to sunrise and sunset. Ten species were caught on separate occasions at intervals of one to three months. During this period the time at which most were flying changed by an interval approximately equal to the change in the time of sunset (fig. 9). Figures 10, *a* and *b* illustrate this point for *Mycetophila ocellus* and *Kimmisia subnebulosa*.

In summer, when cold is least likely to inhibit flight, many strictly crepuscular species had two periods of activity, at dawn and dusk, e.g. *Drosophila disticha* (fig. 10, *e, f*) and *Anisopus fenestralis* (fig. 10, *c, d*). Other species, which respond less critically to light intensity, flew for longer periods in the early morning or late afternoon, e.g. *Thaumatomyia notata* (fig. 10, *g, h*), or during the day with a single skew or unequally bimodal distribution, e.g. *Pericoma nubila* (fig. 10, *j, k*). In the shorter autumn and winter days with less light and lower temperatures, the separate peaks became closer together and eventually overlapped, so that the same species may have a single or skew flight periodicity curve in winter and an extended or bimodal one in summer. Thus

Dyson-Hudson (1956) found that *Drosophila subobscura* had a different pattern of activity in summer, when light was the deciding factor, and in early spring or late autumn, when light became subsidiary to temperature changes. In Quebec, most *Simulium* spp. were caught one to two hours before dawn and half an hour to an hour before sunset. The numbers caught depended on light intensity as long as the temperature was above 7° C., the R.H. above 50 per cent. and the wind speed below 2 m.p.h. (Wolfe & Peterson, 1960).

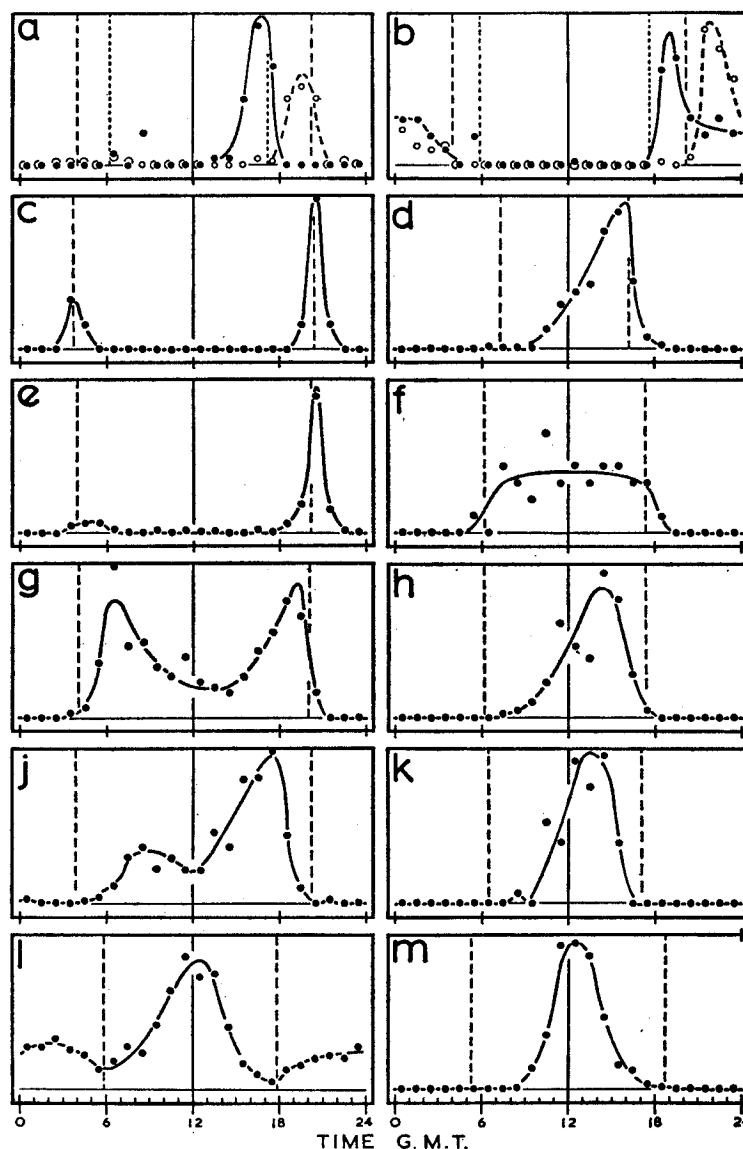


FIG. 10.—Seasonal changes in periodicity curves. (a) *Mycetophila ocellus* (Mycetophilidae: Dipt.): ○ in July, ● in October. (b) *Kimminsia subnebulosa* (Hemerobiidae: Neuropt.): ○ in July & Aug., ● in Sept. & Oct. (c) *Anisopus fenestralis* (Anisopidae: Dipt.) in June. (d) *Anisopus fenestralis* (Anisopidae: Dipt.) in November. (e) *Drosophila disticha* (Drosophilidae: Dipt.) in July. (f) *Drosophila disticha* (Drosophilidae: Dipt.) in October. (g) *Thaumatomyia notata* (Chloropidae: Dipt.) in July. (h) *Thaumatomyia notata* (Chloropidae: Dipt.) in October. (j) *Pericoma nubila* (Psychodidae: Dipt.) in June & July. (k) *Pericoma nubila* (Psychodidae: Dipt.) in October. (l) *Aleyrodes proletella* (Aleyrodidae: Hem.) in September. (m) *Aleyrodes proletella* (Aleyrodidae: Hem.) in October.

The whitefly *Aleyrodes brassicae* (= *proletella*) is unusual because the timing of its peak activity seems to be independent of light intensity only in certain seasons. Maximum numbers of the autumn generation may be caught at any time during the day or night so long as the temperature remains above 9° C. (figs. 2, *b*; 10, *l, m*), but the summer generations did not fly at night even at much higher temperatures (El Khidir, 1963).

#### VII. FOOD, HABITAT AND TIME OF FLIGHT

When the insects caught were classified according to their adult feeding habits and separated into day, crepuscular and night-flyers, striking differences appeared (Table I). Predators, flower-feeders and particularly leaf-feeders were predominately day-flyers, presumably because their food is detected mostly by sight. In contrast, most species feeding on decaying organic matter flew at dawn, or more especially at dusk, when the air is frequently still and moist and food might be easily detected by scent.

TABLE I.—*The relationship between time of flight and adult feeding habits*

Adult feeding category	No. of examples	Percentage flying		
		Day	Dawn & Dusk	Night
Predators . . . . .	54	69	22	9
Leaf-feeders . . . . .	79	96	4	0
Flower-feeders . . . . .	142	70	19	11
Feeders on decaying organic matter . . . . .	151	46	52	2
Non-feeders . . . . .	25	24	0	76

In the daytime, scents probably spread further, disseminated by vertical and horizontal air currents, but they are consequently more diluted and their gradients less definite. In addition, insects that detect scents from downwind will have greater difficulty in flying upwind to the source. The air is least turbulent and most humid just before dawn, but temperature is then at its lowest, and evaporation of scents is probably less than in the evening. Species associated with fungi often flew at dawn and dusk, whereas those associated with vegetable breakdown were more often limited to dusk flight. Most non-feeders were active at night, when the evaporation rate is least, perhaps because of their need to conserve water.

All the insects caught were designated large or small, *i.e.* > or < 30 mm.<sup>2</sup> (see Taylor, 1962). Thirty per cent. of the 274 taxa of small insects and 35 per cent. of the 203 taxa of large insects flew by day, but this difference was not significant ( $P > 0.05$ ).

Groups of different sized individuals were also separated according to the kind of site at which the insects were collected. Of the 240 taxa caught in pre-climax vegetation (on agricultural land), 72 per cent. were composed of small insects (< 30 mm.<sup>2</sup>), whereas of the 234 taxa caught in climax vegetation (on non-agricultural land), only 42 per cent. were similarly composed (41 per cent. in climax woodland and 44 per cent. in waterside climaxes).

In agricultural habitats, the Nematocera (Diptera) were the commonest group; they were relatively rare in ancient woodland. These differences in the faunal composition between areas of permanent (climax) vegetation and agricultural (pre-climax) vegetation are probably the result of long cultural practice, which has encouraged insects associated with the rapid breakdown of organic matter; these insects tend to be small. The proportion of day-flying insects in the agricultural habitats was similar to that in the non-agricultural, being 71 per cent. and 64 per cent., respectively, but as many of the species found in agricultural habitats are composed of insects in the smaller size category, they will be more prone to random, windborne dispersal which, together with a rapid reproduction rate, is characteristic of many important pests.

Of 69 species, which are troublesome enough to agriculture and horticulture in the



United Kingdom to merit publication of an advisory leaflet by the Ministry of Agriculture, and the flight times of which are known, 56 (81 per cent.) are day-flyers and 13 (19 per cent.) night-flyers. The night-flyers include 10 moths (see p. 425) and if all Lepidoptera are excluded, 94 per cent. of pests are day-flyers. There is a larger percentage of day-flyers amongst pest species than is general for populations living in agricultural habitats.

### VIII. FLIGHT PERIODICITY AND MIGRATION

#### *High Altitude and Long Range Migration*

The stability of the air changes during the 24-hour cycle. Figure 11, drawn from data obtained over three years by Best, Knighting, Pedlow & Stormonth (1952), shows

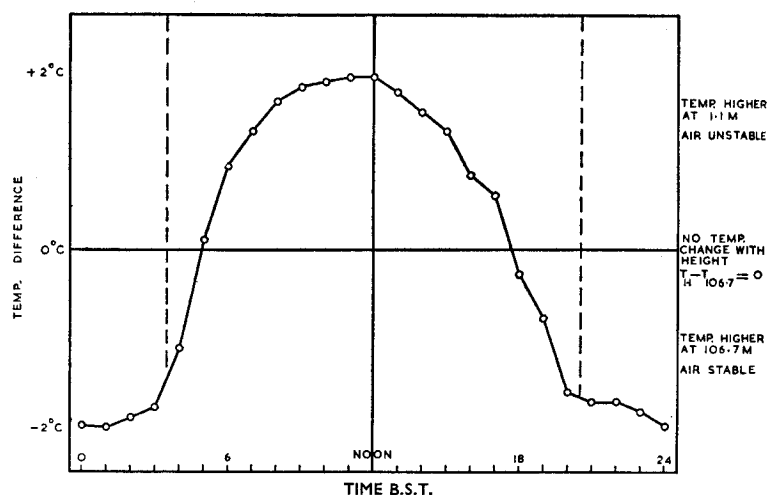


FIG. 11.—Mean hourly cycle of the difference between the air temperature at 1.1 m. and that at 106.7 m. during the month of June in the years 1946/7/8 at Rye, Sussex, England, 50° 58' 21" N., 0° 48' 16" E., over flat country 3.8 m. above sea level.

changes in the mean lapse rate throughout the day in June. At night, when the temperature is maximal at high altitudes, the air is more stable than in the daytime, when the lower air is warmest. Thus the time of flight is important for insect migration and dispersal, because insects that take off in the daytime are more likely to be carried into the upper air by turbulence and convection and to be transported over longer distances than those flying at dawn, evening and night in more stable air (Johnson, 1957a; Taylor, 1958), which probably move more locally.

Insects have been caught at all heights in the air up to 15,000 feet (Freeman, 1945; Glick, 1939; Hardy & Milne, 1938; Johnson, 1957b; Taylor, 1960) and at great distances from possible sources (Yoshimoto, Gressitt & Mitchell, 1962). Yoshimoto *et al.* (t.c.) trapped insects on ships at sea and from aeroplanes in the south Pacific and Antarctic. All the insects caught must have been carried into the upper air and over the sea by wind and had probably been airborne for hours, and possibly for days. We do not know from what parent population these migrant insects originated. However, Hardy & Milne (1938) and Freeman (1945) sampled the air up to 2000 feet, over south-eastern England, and the population from which their migrant insects came was probably much the same as ours. Our own material enables us to classify many families as predominately day-flying or night-flying. These classified samples are not taken randomly, for we have selected our original material. However, this selection merely excluded insects that were unidentifiable or already well represented, and there is no reason to suppose that the proportion of day- and night-flying families

*Trans. R. ent. Soc. Lond.* 116. (15). Pp. 393–476, 18 figs. 1964. 19

has been much affected. The log. of the number of individuals in the families of small day-flying insects caught by us is still highly correlated ( $P < 0.001$ ) with those caught by Freeman (data in Table II, part 1). It is therefore reasonable to regard our species as representing the ground level or resident population from which came the migrants represented by the samples of Hardy & Milne and Freeman, and the migrating insects caught by Yoshimoto *et al.* also possibly originated from resident populations in which the same major families as caught in the present work predominated.

TABLE II.—Comparison of the number of insects caught in four samples

Order/family	(a) Small day-flyers			
	Lewis & Taylor (present paper)	Freeman (1945)	Hardy & Milne (1938)	Yoshimoto <i>et al.</i> (1962)
Psocoptera . . .	694	2355	1	0
Thysanoptera . . .	37,062	623	16	10
Hemiptera				
Lygaeidae . . .	4	16	1	0
Tingidae . . .	4	52	0	0
Anthocoridae . . .	1001	10	0	0
Bythoscopidae . . .	229	0	0	0
Jassidae . . .	794	333	15	0
Typhlocyidae . . .	1016	0	0	0
Chermidae . . .	58	229	7	12
Aphididae . . .	74,693	5810	124	614
Lepidoptera				
Glyphipterygidae . . .	190	0	0	0
Coleoptera				
Hydrophilidae . . .	854	44	1	0
Leiodidae . . .	40	0	0	0
Clambidae . . .	76	0	0	0
Scydmaenidae . . .	21	0	0	0
Ptiliidae . . .	1999	11	0	0
Staphylinidae . . .	6128	548	13	1
Dermestidae . . .	49	0	0	0
Nitidulidae . . .	1174	18	0	1
Cucujidae . . .	441	0	0	0
Lathridiidae . . .	300	299	0	0
Anthicidae . . .	92	0	0	0
Chrysomelidae . . .	271	178	24	0
Strepsiptera				
Elenchidae . . .	15	0	0	0
Hymenoptera				
Braconidae . . .	1795	411	17	6
Aphidiidae . . .	665	1502	8	0
Chalcididae } . . .	2050	1087	1	20
Encyrtidae } . . .				
Pteromalidae . . .	159	0	26	1
Eulophidae . . .	2853	0	11	5
Mymaridae . . .	1217	66	0	0
Proctotrupoidea . . .	619	647	4	0
Diptera				
Scatopsidae . . .	1783	0	0	0
Sciarinae . . .	2195	2486	92	0
Phoridae . . .	76,996	340	8	5
Opomyzidae . . .	160	0	0	0
Ephydriidae . . .	85	254	22	31
Sphaeroceridae . . .	7555	1054	14	11
Agromyzidae . . .	350	281	6	183
Chloropidae . . .	6985	1795	34	8
Totals				
No. of families . . .	39	25	20	14
No. of insects . . .	232,682	20,449	445	908

(b) *Large day-flyers*

Order/family	Lewis & Taylor (present paper)	Freeman (1945)	Hardy & Milne (1938)	Yoshimoto <i>et al.</i> (1962)
Odonata				
Coenagriidae . .	20	0	0	0
Hemiptera				
Miridae . . . .	342	0	0	0
Tettigoniellidae .	34	0	0	8
Megaloptera				
Sialidae . . . .	31	0	0	0
Trichoptera				
Polycentropidae .	42	0	0	0
Hydroptilidae . .	26	0	0	0
Lepidoptera				
Nymphalidae . . .	21	0	0	0
Pieridae . . . .	71	0	1	0
Hesperiidae . . .	12	0	0	0
Coleoptera				
Cantharidae . . .	379	0	0	0
Elateridae . . . .	44	0	0	0
Helodidae . . . .	69	0	0	0
Byturidae . . . .	88	0	0	0
Coccinellidae . .	2	0	0	4
Mordellidae . . .	133	0	0	0
Curculionidae . .	734	86	0	2
Hymenoptera				
Tenthredinidae . .	404	3	0	0
Formicidae . . . .	1	13	0	17
Vespidae . . . . .	174	0	0	0
Apidae . . . . .	703	0	0	0
Diptera				
Ptychopteridae . .	123	0	0	0
Bibionidae . . . .	674	0	0	0
Stratiomyidae . .	40	0	0	0
Rhagionidae . . .	46	0	0	0
Asilidae . . . . .	30	0	0	0
Empididae . . . .	1495	132	3	0
Dolichopodidae . .	2212	0	0	0
Dorilaidae . . . .	73	0	0	0
Syrphidae . . . . .	3354	0	0	1
Pallopteridae . .	26	0	0	0
Trypetidae . . . .	71	0	0	2
Lauxaniidae . . .	18	0	0	0
Sepsidae . . . . .	3025	0	1	0
Helomyzidae . . .	12	0	0	1
Cordiluridae . . .	1280	0	2	0
Calliphoridae . .	800	0	0	0
Muscidae . . . . .	1790	0	1	7
Totals				
No. of families . .	37	4	5	8
No. of insects . .	18,399	234	8	42

(c) *Small night-flyers*

Order/family	Lewis & Taylor (present paper)	Freeman (1945)	Hardy & Milne (1938)	Yoshimoto <i>et al.</i> (1962)
Neuroptera				
Coniopterygidae .	97	0	1	0
Sisyridae . . . .	88	0	0	0
Lepidoptera				
Elachistidae . . .	113	0	0	0
Coleophoridae . .	322	0	0	0
Gracillariidae . .	12,414	0	0	0

(c) *Small night-flyers—contd.*

Order/family	Lewis & Taylor (present paper)	Freeman (1945)	Hardy & Milne (1938)	Yoshimoto <i>et al.</i> (1962)
Plutellidae . . .	213	0	0	0
Adelidae . . .	20	0	0	0
Diptera				
Mycetophilinae . .	2663	0	0	1
Totals				
No. of families . .	8	0	1	1
No. of insects . .	15,930	0	1	1

(d) *Large night-flyers*

Order/family	Lewis & Taylor (present paper)	Freeman (1945)	Hardy & Milne (1938)	Yoshimoto <i>et al.</i> (1962)
Ephemeroptera				
Ephemerellidae . .	64	0	0	0
Neuroptera				
Hemerobiidae . . .	193	0	0	0
Chrysopidae . . .	104	0	0	0
Trichoptera				
Psychomyiidae . .	23	0	0	0
Lepidoptera				
Caradrinidae . . .	546	0	0	4
Plutidae . . .	246	0	0	0
Sterrhidae . . .	76	0	0	0
Hydriomenidae . .	78	0	0	0
Crambidae . . .	860	0	0	0
Pyraustidae . . .	62	0	0	0
Alucitidae . . .	81	0	0	0
Tortricidae . . .	337	0	0	0
Eucosmidae . . .	406	0	0	0
Oecophoridae . . .	20	0	0	2
Diptera				
Tipulidae . . .	3256	0	1	0
Trichoceridae . .	1822	0	0	0
Totals				
No. of families . .	16	0	1	2
No. of insects . .	8174	0	1	6

In Table III these four samples are compared, and the insects divided into four categories, small and large, and day- and night-flyers. The table shows that the results obtained by Hardy & Milne, Freeman, and Yoshimoto *et al.* are much alike, and that the data obtained by these authors may be combined as representing migrants, as a class. The small day-flyers occurred more often at high altitudes and over the sea than did large day-flyers or night-flyers, but direct comparison is made difficult because our sample is much bigger than the others. The samples differ in size, time and place of collection, and the ratios are therefore not absolute values. However, expressed as

TABLE III.—*Summary of data shown in Table II*

	Day-flyers		Night-flyers	
	Small	Large	Small	Large
No. of insects in sample				
Residents (Lewis & Taylor) . .	232,682	18,399	15,930	8174
Migrants (Hardy & Milne + Freeman + Yoshimoto <i>et al.</i> )	21,802	284	2	7
Ratio of migrants to residents . .	0.093699	0.015435	0.000126	0.000856
Ratio as % of small day-flyers . .	100	16.5	0.1	0.9

a percentage of the largest group, they indicate the relative commonness of migrants compared with residents in each of the four categories (*see* Table III).

The small day-flying insect is between 100 and 1000 times as likely to migrate long distances as the night-flying insect and about six times as likely as the large day-flyer. Any effect of size on migration of night-flyers cannot be detected in these meagre data. The results obtained within the Mycetophilidae are typical: Hardy & Milne and Freeman found that high altitude migrant Mycetophilids were small, dark, day-flying Sciariinae.

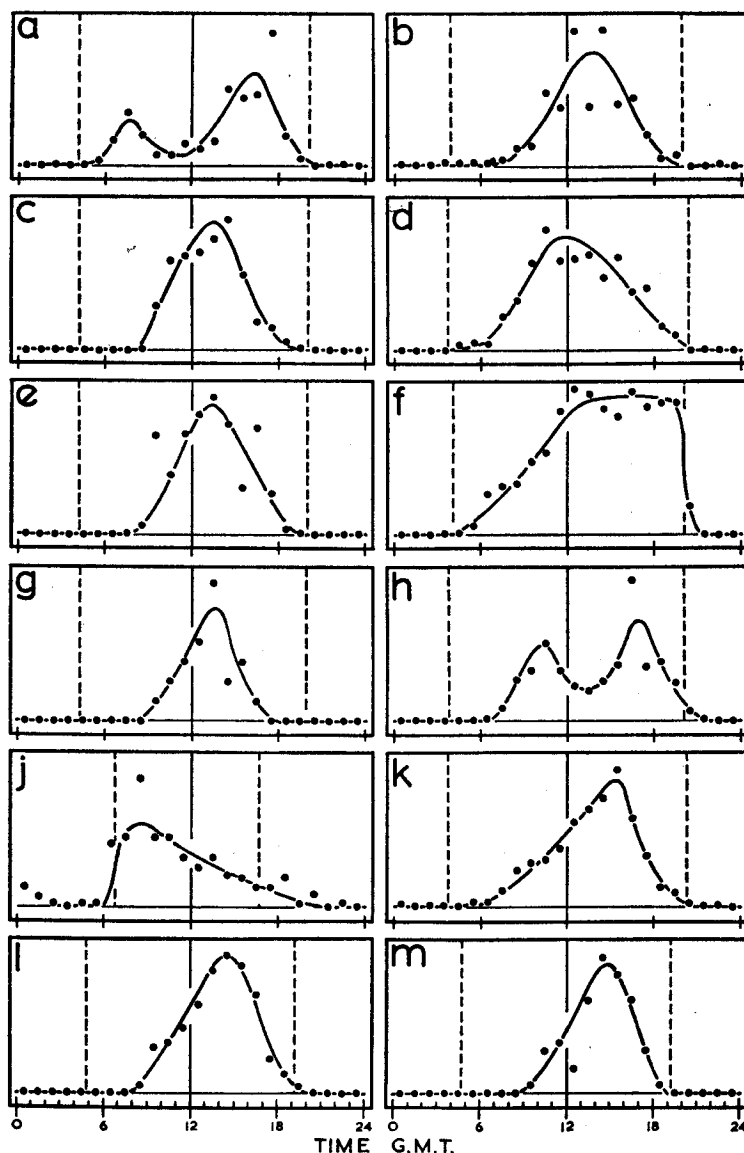


FIG. 12.—Examples of periodicity curves for small, probably migratory, day-flyers. (a) Mixed Ptiliidae (Col.); (b) *Rhynchaenus fagi* (Curculionidae: Col.); (c) mixed Platygasteridae (Hym.); (d) mixed Myrmecidae (Hym.); (e) *Ceranisus menes* (Eulophidae: Hym.); (f) *Trioxys angelicae* (Aphididae: Hym.); (g) *Trioza urticae* (Chermidae: Hem.); (h) mixed Aphididae (Hem.); (i) *Stenopsocus immaculatus* (Stenopsocidae: Psocopt.); (k) *Oscinella frit* (Chloropidae: Dipt.); (l) mixed Thripidae (Thysanopt.); (m) *Phlaeothrips coriaceus* (Phlaeothripidae: Thysanopt.).

Synchronisation of the life cycle and distribution of many small parasitic Hymenoptera (fig. 12, *c, d, e, f*) with their homopterous (fig. 12, *g, h*) and day-flying lepidopterous hosts is assisted by the occurrence of the flight activity of both host and parasite in the daytime, when they are subjected to the same distributive processes. Daytime flights assure the dispersal of many small insects that lack the ability to fly over long distances unless assisted by wind, *e.g.* Thysanoptera (fig. 12, *l, m*) (Lewis, 1959*a*), Chloropidae (fig. 12, *k*) (Johnson, Taylor & Southwood, 1962), Psocoptera (fig. 12, *j*), Ptiliidae (fig. 12, *a*), Mymaridae (fig. 12, *d*) and small Curculionidae (fig. 12, *b*).

#### *Migration and the Flight Curve*

The shape of the flight periodicity curve for individual species undoubtedly results not only from the proximity of traps to populations and food but also from the interaction of many physical and physiological factors, *e.g.* light intensity, temperature, season, age and sexual maturity of the insects. It is therefore impossible to relate the shape of curves to any single factor, but the shape of some suggests that one of these contributory factors may predominate. For instance, in day-flying insects, the shape of the flight periodicity curve at ground level may perhaps occasionally indicate whether the population is migratory. Protracted, flat-topped curves were often associated with populations of fairly constant numbers of the same individuals flying in a restricted area. For instance, Empididae, which were seen flying steadily back and forth over nettle clumps, a pond and a very small heath (fig. 3, *j*) and *Phaonia rufipalpis*, flying over a small pond (fig. 1, *f*), produced this flat-topped flight periodicity curve. These insects are fairly strong flyers, and their observed behaviour suggested that a local population was flying around a limited habitat in search of food. In contrast, insects from a population known to be migrating, which appeared to fly upwards at take-off and quickly drift from sight, *e.g.* aphids, thrips, Chloropids and hymenopterous parasites, often produced a more normally-distributed flight periodicity curve. A third type of curve, which shows a long period of limited flight activity followed or preceded by a sudden increase, *e.g.* *Stenopsocus immaculatus* (fig. 12, *j*) or *Macrosteles sexnotatus* (fig. 15, *k*), might therefore indicate a mixed population of insects of different flight capability, habits, and perhaps age, or even a mixture of migratory and non-migratory individuals.

The absence of a light threshold in the autumn generation of *Aleyrodes proletella* appears to distinguish it from earlier generations (El Khidir, 1963). Such an adaptation in a migratory generation could be valuable for insects that migrate long distances over sea. For example, *Laphygma exigua* Hübn., which flies from N. Africa to S. England (Hurst, 1963; French, 1964) and must continue to fly in light and darkness, and *Plutella maculipennis*, which usually flies in the late evening (*Appendix B*), are also carried in the wind for many days over great distances (French & White, 1960).

Temperature inversion of the air might assist the nocturnal dispersal of moths. At twilight, females of *Loxostege sticticalis* L. are alleged to be carried up to 7–8 metres by currents of warm air when nocturnal inversion develops as the air near the surface of the ground cools rapidly (Mel'nichenko, 1936). The zone of temperature suitable for flight, 25–28° C., gradually rises during the night, so that the moths eventually reach 75–100 metres. Some are then likely to be carried in the air that may be moving at these altitudes even when it is motionless below. Larsen (1948) observed similar behaviour in *Plusia gamma*. This aspect of flight behaviour is important in agriculture, for 10 of the 13 most important night-flying pests in Britain are moths.

#### *Migration and Temporary Habitats*

Southwood (1962) showed that inhabitants of temporary habitats tend to be migrants. Insects from temporary habitats provide 423 out of 451 (94 per cent.) of our periodicity curves, even though many were caught in sites with climax vegetation.

This may indicate that most of the flight we measured is migratory. We showed that long distance migration is highly correlated with day flight (*see* p. 410). Day-flyers constituted 65 per cent. of the insects from temporary habitats but only 43 per cent. of those from permanent ones. Thus day-flight, temporary habitats and long distance migration are all correlated, but time of flight is also correlated to adult feeding habits, as shown in Table I, which includes many night-flyers. Even these may be migratory, although their flight is self-powered and of short duration and range. Migration is the movement, in this instance by flying adults, from old to new breeding sites. Most

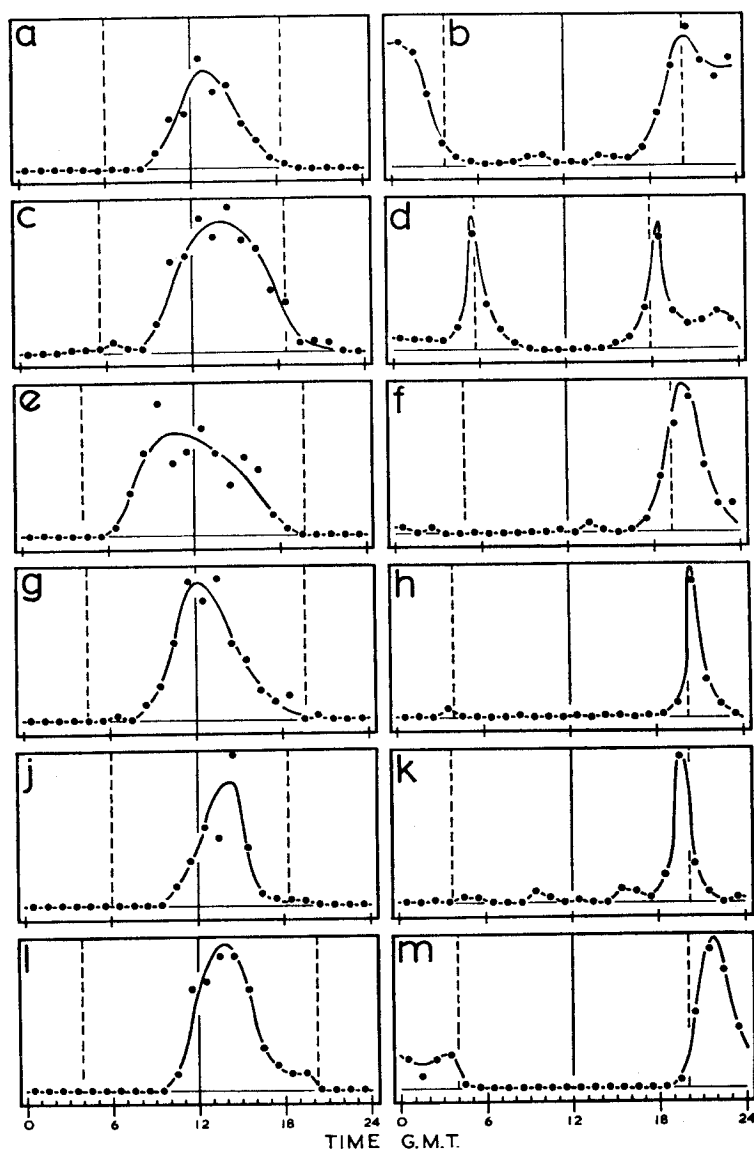


FIG. 13.—The periodicity curves for dark-coloured, day-flying Nematocera (*a, c, e, g, j, & l*) contrasted with the curves for pale-coloured night-flying species (*b, d, f, h, k, & m*). Cecidomyiidae: (*a*) mixed Lestremiinae; (*b*) mixed Cecidomyiinae. Mycetophilidae: (*c*) mixed Sciarinae; (*d*) *Mycetophila fungorum*. Psychodidae: (*e*) *Pericoma* sp.; (*f*) *Psychoda alternata* and *Telmatoscopus ustulatus*. Culicidae: (*g*) *Chaoborus crystallinus*; (*h*) *Culex pipiens*. Chironomidae: (*j*) *Hydrobaenus foliaceus*; (*k*) *Tanytarsus atrofasciatus*. Ptychopteridae: (*l*) *Ptychoptera contaminata*. Tipulidae: (*m*) *Tipula* sp.

crepuscular-and night-flyers feed as adults on decaying organic material (Table I) and oviposit in the same medium. Hence feeding and migratory flight may be indistinguishable with these insects and these data. The comments on *Neuroterus quercus-baccarum* mentioned in the section on Hymenoptera (p. 427) are also relevant in this context.

#### IX. COLOUR IN RELATION TO DAY AND NIGHT FLIGHT

##### *Colour in the Nematocera*

The night-flying Nematocera (Diptera) were mostly pale in colour and contrasted sharply with the dark day-flyers (fig. 13). We found examples in the Culicidae, Chironomidae, Psychodidae, Cecidomyiidae, Mycetophilidae, the generally pale

TABLE IV.—*Lightness of colour in different species of Nematocera (Diptera) compared with the light intensity at the time of mean flight activity*

Species	Mean Munsell values	Light intensity at time of mean flight activity
Tipulidae		
<i>Nephrotoma quadrifaria</i>	4.5	25
<i>Ormosia nodulosa</i>	2.5	5000
<i>Empeda cinerascens</i>	4.5	360
<i>Tipula</i> sp.	5.5	0.05
Trichoceridae		
<i>Trichocera annulata</i>	3.5	600
Ptychopteridae		
<i>Ptychoptera albimana</i>	1.0	8400
Psychodidae		
<i>Pericoma nubila</i>	2.0	6200
<i>Psychoda phalaenoides</i>	6.0	8
<i>Psychoda brevicornis</i>	4.5	930
Culicidae		
<i>Chaoborus crystallinus</i>	3.0	8000
<i>Culex pipiens</i>	5.75	0.1
Chironomidae		
<i>Pentaneura nubila</i>	3.0	520
<i>Hydrobaenus foliaceus</i>	2.0	5500
<i>Tanytarsus tenuis</i>	4.75	930
<i>Tanytarsus manicus</i>	7.25	1.0
Ceratopogonidae		
<i>Forcipomyia bipunctata</i>	2.5	600
<i>Culicoides obsoletus</i>	2.5	104
Bibionidae		
<i>Dilophus febrilis</i>	1.25	9500
Scatopsidae		
<i>Psectrosciara tenuicauda</i>	1.0	9000
<i>Swammerdamella brevicornis</i>	1.75	9000
Mycetophilidae		
<i>Allodia</i> sp.	3.5	570
<i>Mycetophila ocellus</i>	4.0	570
Mycetophilinae	5.5	0.4
Mycetophilinae	4.25	600
Sciarinae	2.0	4700
Cecidomyiidae		
Lestremiinae	3.25	7000
Cecidomyiinae	6.5	0.03

The degree of lightness or darkness of the insects was determined by two independent observers using hues 5 YR and 10 YR on a Munsell colour chart. In this system the value extends from a theoretically pure black, symbolised as 0, to theoretically pure white, symbolised as 10. A grey or chromatic colour that appears visually halfway in lightness between pure black and pure white has a value of 5. The mean of the values determined by the two observers is given.



nocturnal Tipulidae and the dark day-flying Ptychopteridae. Day-flyers may be uniformly black, e.g. *Hydrobaenus foliaceus* (Chironomidae) and *Pericoma fusca* (Psychodidae), black flecked with paler colours, e.g. *Pericoma nubila*, or dark brown, e.g. *Chaoborus crystallinus* (Culicidae), Sciarinae and Lestremiinae. The night-flyers are of many colours: pale green, e.g. *Tanytarsus tenuis* (Chironomidae); pale orange, yellow or brown, e.g. many Cecidomyiinae, *Mycetophila fungorum* (Mycetophilidae), *Culex pipiens* (Culicidae); pale grey, e.g. *Psychoda alternata* (Psychodidae); or almost translucent, e.g. *Tanytarsus atrofasciatus* (Table IV). The only evidence found of a similar division in another order was in the family Nitidulidae (Coleoptera), in which the dark *Meligethes* spp. flew by day, but a pale brown species of the genus *Epuraea* flew in the late afternoon.

#### Colour, Light and Temperature

Difference in colour between day- and night-flying species has been noticed before (Shannon, 1931; Kalmus, 1941), though not so extensively as in these Nematocera. Its prevalence in this group suggests that it has some ecological significance other than a protective adaptation of the kind usually associated with colour (Cott, 1957). Kalmus (1941) suggested that dark colour in insects was associated with resistance to desiccation. Tanning of the cuticle can provide a degree of impermeability to water (Lafon, 1943), and Koidsumi (1934) suggested a correlation between the hardness, and blackness, of cuticle and its impermeability, but Wigglesworth (1948) concluded that the impermeability of hard cuticle to water was independent of its thickness and sclerotisation. Also, much of the colour variation in Nematocera is of pigmentary rather than cuticular origin, so that the different colours of day- and night-flying species appear to be unrelated to humidity. They may, however, be related to radiation and light intensity.

Thus dark colour may be advantageous for insects that require high temperatures for flight in the daytime, because exposure to radiation raises body temperature above the ambient temperature. Buxton (1924) found that the brown race of the Acridiid *Calliptamus* had a body temperature 4–5° C. higher in sunshine than the buff race of the same species, and similar differences occur between the body temperature of black and green *Locusta* hoppers (Uvarov, 1948). In contrast Digby (1955) considered that the effect of colour in increasing radiation temperature in insects was slight. He concluded, from his own direct measurement and from the absorptivity measurements of Rücker (1933, *a* & *b*; 1934) and Duspiva & Cerny (1934), that in insects that differ only in colour, the increase in temperature of chalky-white forms would be 52 per cent. of that of the darkest forms, whereas in blue, green and yellow insects the increase would probably be 75 per cent. In absolute terms, dark coloration may thus produce a temperature increase of only 1–2° C. in small insects, but even such a small rise could help an insect to warm its body enough for flight. At night, dark colour would increase the loss of heat by radiation (Rücker, 1933*a*), and the number of occasions suitable for flight would be fewer, but this radiation loss is very small. An equally plausible explanation for the colour differences is that dark colours give protection against ultra-violet radiation (Prochnow, 1929; Schröder, 1927), which is not experienced by night-flyers. This is supported by the fact that with most Nematocera the whole insect is either dark or pale and not the thorax alone, which is all that would be needed to raise the muscular temperature solely for flight.

At high altitudes, where cold and ultra-violet radiation are greater hazards, insects are darker and smaller (Mani, 1962). Melanism increases protection against both cold and ultra-violet, but any gain in temperature might well be off-set by the smaller size, which makes it more difficult to maintain a body temperature different from the ambient. This is reflected in the present material by the day-flying *Hydrobaenus*, Lestremiinae and Sciarinae, which are smaller and darker than the night-flying Chironomidae, Cecidomyiinae and Mycetophilinae. The Sciarinae and the Lestremiinae

are considered to be the primitive members of their respective families. Day flight is likely also to be primitive, and the evolutionary trend in the Nematocera may well be from small, dark, day-flyers to larger, paler, night-flyers. In a large sample of 120 species of Nematocera, 37 per cent. were found to be day-flyers (Table V). This contrasts sharply with the samples of the other Diptera; *e.g.*, Brachycera with 100 per cent. day-flyers and Cyclorrhapha with 91 per cent. Nematocera are notably poor flyers, and evolutionary pressure may lead to their flying at night when wind-speed is less and, possibly, predators are fewer. Though the temperature is also lower, the absence of ultra-violet light, the slight gain in temperature engendered by loss of

TABLE V.—*The proportion of day-flying species in different taxa.*

Insect orders	Percentage day-flyers*	No. in sample
Paleopteroides		
Ephemeroptera . . . . .	52	1 + 20 (Harris, 1952)
Odonata . . . . .	70	1 + 19 (Corbet, 1961)
Oligoneopteroides		
Coleoptera . . . . .	92	81
Megaloptera . . . . .	100	1
Planipennia (Neuroptera) . . . . .	0	7 + 41 (Withycombe, 1922)
Hymenoptera . . . . .	94	49
Strepsiptera . . . . .	100	1
Mecopteroides		
Cyclorrhapha . . . . .	91	74
Brachycera . . . . .	100	32
Nematocera . . . . .	37	120
Mecoptera . . . . .	100	1
Trichoptera . . . . .	33	3 + 9 (Crichton, <i>in litt.</i> )
Lepidoptera (suction trap) . . . . .	15	52
Macrolepidoptera . . . . .	15	837 (South, 1939, 1945)
Paraneopteroides		
Thysanoptera . . . . .	100	11
Psocoptera . . . . .	75	4
Hemiptera . . . . .	91	67 + 52 (Southwood, 1960)

\* Mean flight activity at light intensities > 1000 f.c.

pigment and the maintenance of the gain made possible by increased size may be enough to make night flight possible. It is not possible in the present material to distinguish conclusively between temperature and light as the basic causative factors, because neither was measured, and they are closely correlated. However, the association between body colour and the light intensity at the time of maximum flight is shown for the Nematocera in figure 14. The relationship is so striking and continuous, from near white in moonlight to black in full sunlight, that it seems most likely that light is the immediate environmental factor that governs body colour, whatever protective mechanism may be involved and whatever evolutionary pressure may make the association necessary. The exposure of *Pieris* pupae to ultra-violet light increases the amount of black pigment, and decapitation of the larvae obliterates this response (Brecher, *in* Wigglesworth, 1953). It may be possible to resolve this problem experimentally by submitting day- and night-flying species in the same family, *e.g.* Cecidomyiidae, to heat and ultra-violet treatment.

#### *Evolution of Night Flight*

If there is any evolutionary trend in time of flight, the proportions of day-flyers in the higher taxa should reflect it. To investigate this we have set out the figures from our own material, supplemented where possible by published data, in Table V, under orders arranged to show evolutionary affiliations (Grassé, 1949). We have no new data for the Polyneoptera, perhaps because flight is less common in this group of

orders than in some others. Thysanoptera appear not to have maintained, or may not have evolved, night flight, and in the Hemiptera it is rare. One or another species of Ephemeroptera and Odonata flies at all times, and the same seems to hold for the Psocoptera, although our evidence for this order is slight. In the two main groups of orders of flying insects that constitute the Oligoneoptera, the segregation is rather curious. The two large orders Coleoptera and Hymenoptera, and possibly the small orders Megaloptera and Strepsiptera, are almost entirely day-flying, but the closely-related Planipennia are exclusively night-flying in this country, although there are some day-flyers in the tropics. However, in the remaining group, the Mecopteroides, the

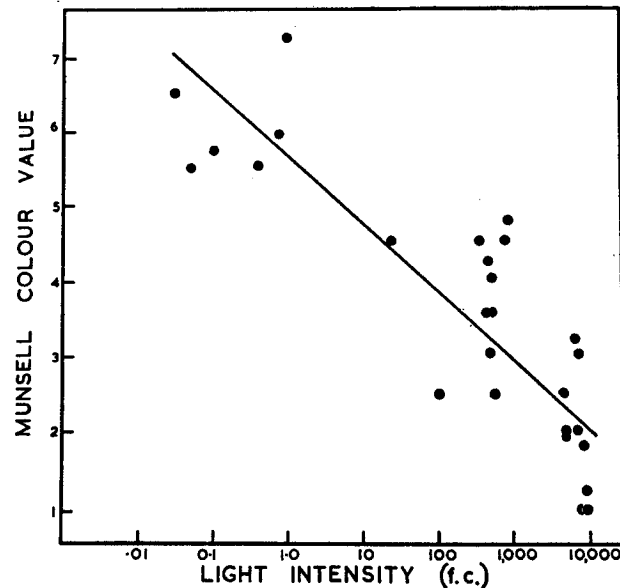


FIG. 14.—The association between body colour and light intensity at the time of maximum flight. The species involved and the procedure used to determine the Munsell colour value are given in Table IV.

segregation is much more uniform: the Cyclorrhapha and Brachycera, and possibly the Mecoptera, are almost exclusively day-flying, but the equally numerous Nematocera, Trichoptera and Lepidoptera contain mainly, but not exclusively, night-flyers. The distinction between the Nematocera and the other flies is very striking.

It is evident that, although night flight has been evolved many times, its appearance in different orders is erratic. In some orders there is widespread adaptation to night flight. The Lepidoptera are furry, the Nematocera are colour-adapted and the nocturnal Trichoptera appear to be larger, paler and less hairy than the day-flyers. In the Brachycera, Cyclorrhapha, Hymenoptera and Coleoptera, however, the relatively few night-flyers do not show similar well developed morphological adaptations, being apparently less plastic in this respect, or more recently evolved. *Drosophila*, *Ophion* and *Melolontha*, in the Cyclorrhapha, Hymenoptera and Coleoptera, respectively, are obviously paler than their day-flying near relatives, but there is no regular trend in these orders as in the Nematocera. The Planipennia as a whole are paler than the day-flying Megaloptera. It will be interesting to see the trends in those orders, especially the Psocoptera and Ephemeroptera, for which we have as yet inadequate evidence.

#### X. SYNOPSIS OF FLIGHT PERIODICITY CURVES

The general characteristics of the periodicity curves for the orders and families adequately represented in our catches are described in this synopsis, and interesting

species or unusual curves are commented upon. References in the literature to flight periodicity determined by non-attractive traps are cited. The complete details of species caught, including the shape of their periodicity curves, time and standard deviation of maximum activity, and the light intensity at which it occurs, are listed in *Appendix B*. Species are arranged in taxonomic order after Kloet & Hincks (1945).

#### DERMAPTERA

We caught only one individual of *Forficula auricularia* L. in our traps, out of a total of about 5 million insects, and this could have fallen in from an overhanging tree. Lucas (1920) cites occasional records of night and day flights by this earwig, and more frequent records of day flight by *Labia minor* L., which sometimes swarms over old dung heaps in sunshine.

#### PSOCOPTERA

Psocids can fly in a wide range of light intensities, from before sunrise throughout daylight until after sunset, but we caught most in the daytime. Many species often migrate soon after emergence (Pearman, 1928), and at times they fly in considerable numbers and drift through the air like winged aphids, although usually the winged forms are "curiously reluctant to take flight" (Imms, 1957). Flight is probably mainly migratory, and is perhaps followed by muscle autolysis as in aphids.

#### EPHEMEROPTERA

The most comprehensive data on times of flight of British Ephemeroptera are given by Harris (1952) (Table VI). Different species are active from early morning until

TABLE VI.—*Day-and night-flying Ephemeroptera, from J. R. Harris (1952)*

Species	Time of flight	
<i>Ephemerella danica</i> Meull. . . .	D	3-4 hrs. before sunset
<i>Paraleptophlebia cincta</i> (Régis) . . .	D	morning, afternoon, early evening
<i>Ephemerella ignita</i> (Poda) . . . .	N	early evening
<i>Ephemerella notata</i> Eaton . . . .	N	early evening
<i>Caenis</i> spp. . . . .	N	dawn and dusk
<i>Baetis scambus</i> Eaton . . . .	D	morning, afternoon
<i>Baetis tenax</i> Eaton . . . .	D	afternoon, early evening
<i>Baetis rhodani</i> (Pictet) . . . .	D	afternoon, early evening
<i>Baetis atrebatinus</i> Eaton . . . .	D	afternoon, early evening
<i>Baetis pumilus</i> (Burmeister) . . . .	D	morning, afternoon
<i>Centroptilum luteolum</i> (Meull.) . . .	D	morning, afternoon, early evening
<i>Cloeon simile</i> Eaton . . . .	D	morning, afternoon
<i>Procloeon rufulum</i> (Meull.) . . . .	N	1 hour before, to 1 hour after, sunset
<i>Siphonurus linnaeana</i> (Eaton) . . . .	N	sunset
<i>Rhithrogena semicolorata</i> (Curtis) . .	D	afternoon until dusk
<i>Heptagenia sulphurea</i> (Meul.) . . .	N	late afternoon until dark
<i>Heptagenia fuscogrisea</i> (Retzius) . .	D	morning, afternoon, early evening
<i>Ecdyonurus venosus</i> (Fabr.) . . . .	N	afternoon, evening
<i>Ecdyonurus dispar</i> (Curtis) : . . .	N	afternoon, evening
<i>Ecdyonurus insignis</i> (Eaton) . . . .	N	late afternoon until dark

N = Night-flying.

D = Day-flying. (Mean flight activity at light intensities >1000 f.c.)

after sunset. Many short-lived species, e.g. *Ephemerella* spp. and *Caenis* spp., are mostly night-flyers and often swarm at sunset (Imms, 1957). The flight period varies from about half an hour in some species flying at sunset, e.g. *Ephemerella ignita* (fig. 15, e), to many hours in those flying throughout the day and early evening, e.g. *Centroptilum luteolum*.

## ODONATA

The first flight of dragonflies is closely related to the time of emergence. Those that emerge at night usually fly at dawn the following morning. Species that emerge in the daytime may fly after an hour, provided the temperature is favourable (Corbet, Longfield & Moore, 1960).

Older insects may fly at any time during the 24 hours, depending on the species, and temperature largely governs the time at which they fly, because adults have upper and lower temperature thresholds for flight (Corbet, 1962). In Europe, *Anax imperator*

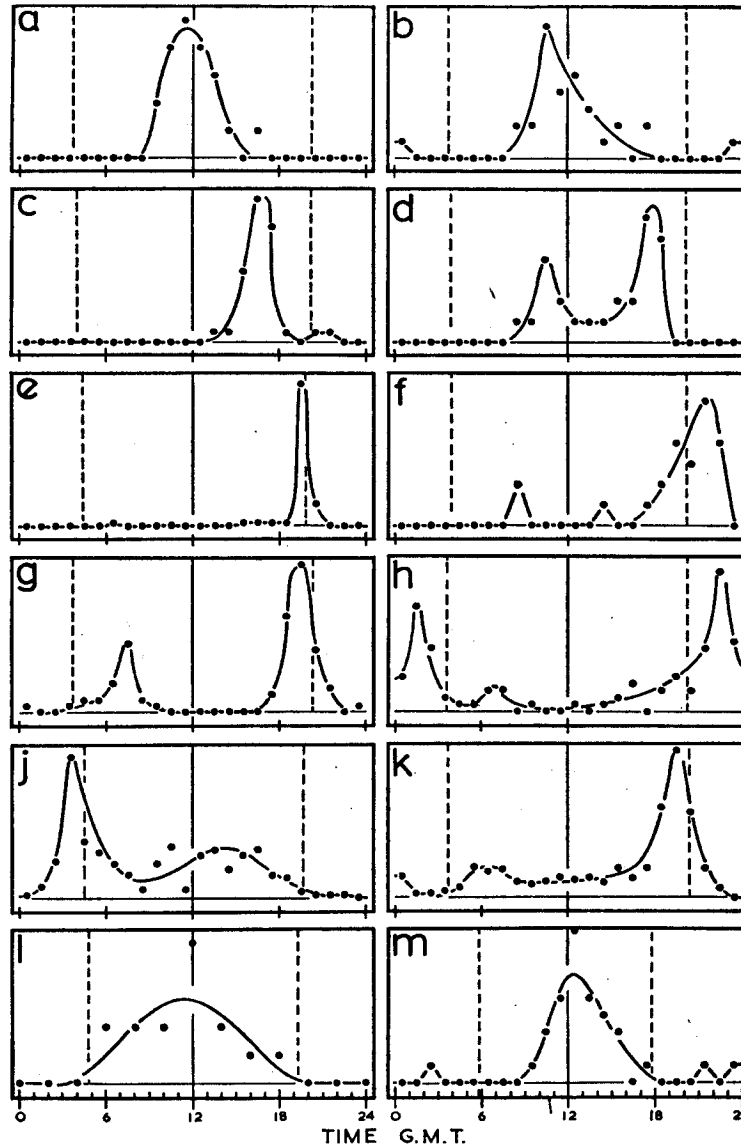


FIG. 15.—Miscellaneous periodicity curves. (a) *Ischnura elegans* (Coenagriidae: Odonata); (b) *Sialis lutaria* (Sialidae: Megalopt.); (c) *Cyrnus trimaculatus* (Polycentropidae: Trichopt.); (d) *Orthotrichia tetensii* (Hydroptilidae: Trichopt.); (e) *Ephemerella ignita* (Ephemerellidae: Ephemeropt.); (f) *Ecnomus tenellus* (Psychomyiidae: Trichopt.); (g) *Sisyra fuscata* (Sisyridae: Neuropt.); (h) *Conwentzia psociformis* (Coniopterygidae: Neuropt.); (j) *Neuroterus quercusbaccarum*, males and agamic generation (Cynipidae: Hym.); (k) *Macrosteles sexnotatus* (Jassidae: Hem.); (l) *Elenchus tenuicornis* (Elenchidae: Strepsipt.); (m) *Graphocephala coccinea* (Tettigoniellidae: Hem.).

Leach usually flies throughout the day (Moore, 1953); the mature males fly mostly at 13.00 hours (Corbet, 1957), but they may rest during the hottest hours in mid-August (Robert, 1958). In Great Britain, most species are day-flyers (Corbet *et al.*, 1960), but in tropical regions there are also many that are crepuscular or fly by night (Corbet, 1962). These belong mostly to the families Aeshnidae and Cordiluridae, although there are also a few crepuscular Zygoptera. They may fly at dawn or dusk or, in some species, at both times.

#### THYSANOPTERA

In all species from the three most common British families, Aeolothripidae, Thripidae and Phlaeothripidae, maximum numbers flew at midday or in the early afternoon, at light intensities of 5000–9500 f.c. There were no differences between the periodicity curves of predatory thrips, flower- and leaf-feeders and fungus-feeders. Occasionally, mass flights of thrips occur, when the weather improves after populations have accumulated during weather unsuitable for flight (Lewis, 1964). Temperature and light intensity are the most important meteorological factors that influence flight; relative humidity and wind are less important (Lewis, 1963).

#### HEMIPTERA

The Hemiptera are predominantly day-flyers and usually have a normal periodicity curve, with a peak between 10.00 and 16.00 hours. In settled weather, this pattern may be altered on single days or over a period, particularly for aphids, by the operation of temperature or light thresholds (Taylor, 1963), or by variation in numbers of the parent population available for flight (Johnson & Taylor, 1957), to produce a bimodal flight periodicity curve. Even so, the different peaks of the diurnal periodicity curves mostly remain normal. Many leafhoppers, however, differ from most other Hemiptera because they are crepuscular, and their periodicity curves are distinctly skew.

The numbers of Heteroptera caught were remarkably few compared with other large orders, totalling approximately 1400; of these, 1000 belonged to species of *Anthocoris* and *Orius*, which appeared to be the commonest and most active genera flying at vegetation level. Relatively few Miridae, which Southwood (1960) considered the most active flyers in the order, were caught. Even when traps were placed among apparently dense populations of the Mirids *Systritotus nigrita*, *Monalocoris filicis* and *Orthotylus virescens*, only 13, 40 and 79, respectively, were caught during 5–7 days. We interpret this to mean that these insects disperse so quickly from their host plants that the traps catch relatively few. Waloff and Bakker (1963) showed that some Miridae from broom are much more active flyers than others. Our results suggest that, compared with most other common flying insects, the Heteroptera considered as a group are among the least active flyers.

Of the 57 British species listed by Southwood (1960), 48 are probably day-flyers and only 9 crepuscular or nocturnal. All the Lygaeidae, Piesmididae, Tingidae and Saldidae from his suction traps were caught in the daytime, but 7 per cent. of the Cimicidae (*sensu* Southwood and Leston, 1959) and 20 per cent. of the Miridae were caught at night. Except for one species, all Heteroptera trapped by us were caught in bright light (7000–9000 f.c.) and the periodicity curves approached normal (fig. 16, *a, b, c*). The exception was the relatively inactive *Orthotylus virescens* (Waloff & Bakker, 1963), which flew mostly at dawn and again at dusk (fig. 16, *d*). Occasional specimens of *Dictyonota strichnocera* Fieber (Tingidae) and *Leptopterna dolabrata* (L.) (Miridae) were caught in the daytime only, but two out of the three specimens of *Mecomma ambulans* Fall. (Miridae) caught were flying at dawn. Glick (1939) caught slightly more Corixidae flying at night than in the daytime, but Macan (1939) found that hot, still days stimulated flight in this family. Allen (1953) recorded Notonectidae in flight during the day.

Aphididae are day-flyers (fig. 12, *h*), and many species exhibited a bimodal flight periodicity curve. These included *Macrosiphum euphorbiae*, *M. rosae*, *M. avenae*,

*Acyrtosiphon onobrychidis*, *Dactynotus jaceae*, *Hyperomyzus lactucae*, *Cavariella aegopodii* (fig. 1, e), *Hyalopterus arundinis*, *Doralis fabae* (fig. 2, a) *Brachycaudus rumexicolens*, *Myzocallis coryli*, *Eriosoma ulmi* and *Semiaphis atriplicis*. *Trioza urticae* (Chermidae) (fig. 12, g) and *Aleyrodes proletella* (Aleyrodidae) (fig. 5, j, k; fig. 10, l, m) were usually day-flyers, with nearly normal curves and maxima around noon, but the autumn form of *A. proletella* has no light threshold and may fly through the night when the temperature exceeds 9° C. (El Khidir, 1963). Müller & Unger (1952) caught more *Trioza nigricornis* at 14.00 hours than at other times, but the yellow water-traps they used may be most effective at this time, thereby influencing the size of the catch.

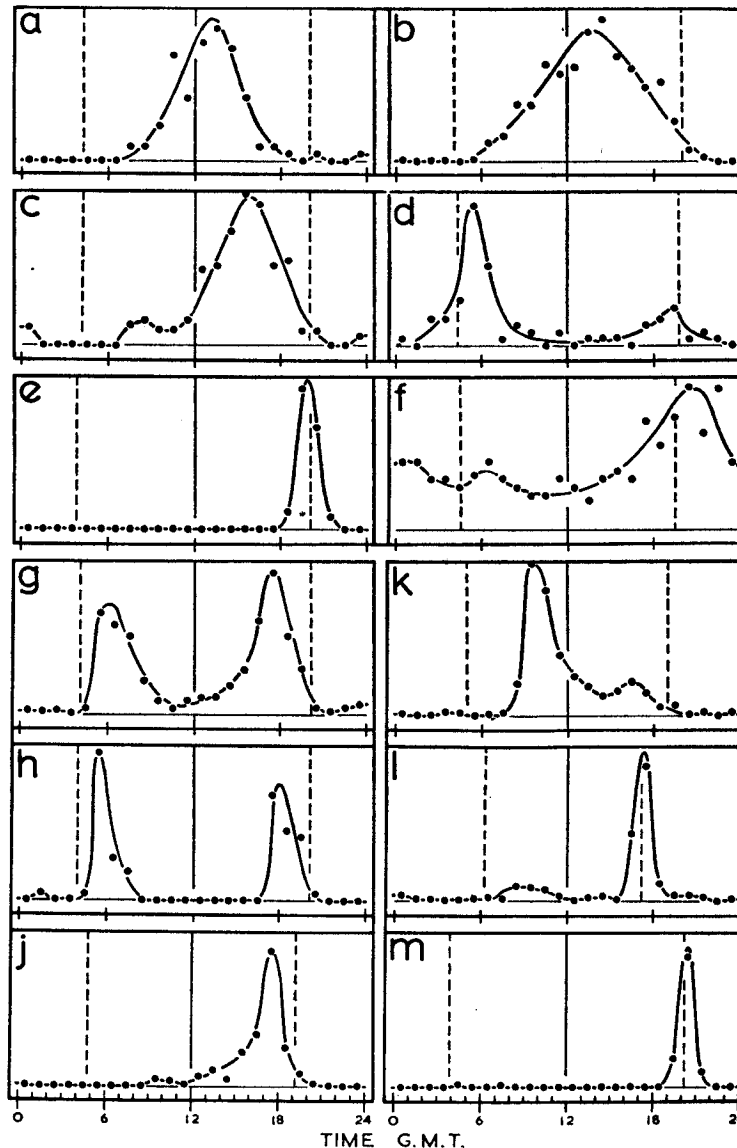


FIG. 16.—Periodicity curves illustrating variation between species within families. Anthocoridae, Hem.: (a) *Anthocoris nemorum*; (b) *Orius* sp. Miridae, Hem.: (c) *Dicyphus epilobii*; (d) *Orthotylus virescens*. Ceratopogonidae, Dipt.: (e) *Culicoides obsoletus*; (f) *C. impunctatus*. Staphylinidae, Col.: (g) *Megarthus depressus*; (h) *M. denticollis*; (j) *Proteinus ovalis*. Chironomidae, Dipt.: (k) *Hydrobaenus semivirens*; (l) *Tanytarsus tenuis*; (m) *Pentaneura nubila*.

The four families of leafhoppers represented in our catches, Tettigoniellidae, Jassidae, Typhlocyidae and Bythoscypidae, included day- and crepuscular-flyers. Day-flyers, e.g. *Graphocephala coccinea* (fig. 15, *m*), usually have a fairly normal periodicity curve, with peak activity around midday (it is interesting to note that *G. coccinea* has been described previously as inactive during the day but attracted to light at night (China, 1935)). The crepuscular species may fly at either dawn or dusk, but many have periodicity curves that are distinctly and characteristically skew. After the dawn peak of flight activity in *Typhlocyba ulmi*, numbers in flight only gradually diminished throughout the day and evening until midnight. Conversely, the late afternoon flight of *Macrosteles sexnotatus* (fig. 15, *k*) was preceded by a steady low activity, starting at dawn. These and similar species can therefore fly in light intensities ranging from starlight (0.00008 f.c.) to midday summer sunlight (8500–9000 f.c.). Lawson, Chamberlin & York (1951), using a rotary trap, found that *Circulifer tenellus* Baker flew at dawn and dusk, providing the temperature was above 15.5–18.0° C. Flying hoppers were most common in the evening, and at very low wind speeds the males swarmed round conspicuous objects.

#### MEGALOPTERA

Only one species, *Sialis lutaria* (Sialidae) (fig. 15, *b*), was caught, and most flew between 10.00 and 13.00 hours.

#### NEUROPTERA (PLANIPENNIA)

Most of the order are crepuscular-or night-flyers (Killington, 1936), even though they have widely different habits and habitats, ranging from the semi-aquatic Osmylidae and the aquatic Sisyridae, which are parasitic on freshwater sponges, to the terrestrial families, e.g. Coniopterygidae, Hemerobiidae and Chrysopidae, which prey mainly on aphids, coccids and mites. The numbers of Hemerobiidae (fig. 10, *b*) and Chrysopidae (Banks, 1952) flying quickly reached a maximum about one hour after sunset and gradually declined throughout the night, with an occasional small resurgence just before sunrise. *Chrysopa carnea* flew occasionally in daylight, especially when disturbed. *Conwentzia psociformis* (fig. 15, *h*) and *Sisyra fuscata* (fig. 15, *g*) both showed two peaks of flight, in the first species in dim light (approx. 0.13 f.c.) after sunset and before sunrise, and in the second before sunset and after sunrise in brighter light (600–2000 f.c.).

Some species of the mainly tropical Ascalaphidae fly during the daytime, but the closely related Myrmeleontidae are crepuscular-flyers (Imms, 1957).

#### MECOPTERA

*Panorpa communis* (Panorpidae) flies during the day, but too few specimens were caught to produce a curve.

#### TRICHOPTERA

The order contains day-flyers (fig. 15, *c, d*), and night-flyers and crepuscular species (fig. 15, *f*). Day-flyers probably predominate in the families Leptoceridae, Hydroptychidae and Hydroptilidae, but many day-flying species fly also in the evening (Crichton, *personal communication*), so they may also be caught in light-traps (Crichton, 1960). According to Brindle (1957), *Mystacides longicornis* (L.), *M. azurea* (L.), *Leptocerus cinereus* Curt., *L. aterrimus* Steph., *Molanna angustata* Curt., *Ecclisopteryx guttulata* (Pict.) and *Hydropsyche angustipennis* (Curt.) are day-flying species, *M. longicornis* and *M. angustata* fly by day and by night, but *Limnephilus rhombicus* (L.), *L. extricatus* McLach., *Phryganea grandis* L., *Oecetis ochracea* (Curt.) and *Halesus digitatis* (Schr.) fly only at night; apart from strong winds, temperature had the most influence on the number flying by night or day. The day-flyers are generally smaller, darker and more hairy than the night-flyers.



## LEPIDOPTERA

Different species of Lepidoptera were active at different times of the day, and their periodicity curves were usually either normal or skewed towards light, and only rarely away from it.

All the Caradrinidae were either evening or night-flyers, and maximum numbers of all species except *Celaena secalis* (fig. 6, c) were caught before midnight. Only *Agrochola lychnidis* had a periodicity curve skewed away from light. The numbers in flight of the Hydriomenidae, Crambidae, Pyraustidae, Tortricidae (fig. 6, o), Eucosmidae (fig. 6, h) and Plutellidae also usually showed a single peak between about one hour after sunset and midnight, and maximum numbers of *Platyptilia pallidactyla* (Alucitidae) (fig. 6, k) were caught at sunset. *Crambus culmellus* consistently flew three hours earlier than *C. hortuellus* and *C. perlellus* (fig. 6, a). The curves for Tortricidae and Eucosmidae were rarely skewed and had a narrower spread than those of most other Lepidoptera. *Elachista cerusella* (Elachistidae) also flew for only a short time at sunset. The Plusiidae were most active 1–2 hours after sunset, with curves skewed towards light, but *Plusia gamma* had an additional flight period before dawn. Larsen (1948), from counts made at 2-hourly intervals of the numbers feeding, also found this species to show a bimodal periodicity curve, with a principal temperature-dependent peak in early afternoon and a light-dependent peak in the evening.

The Nymphalidae (fig. 3, a), Pieridae and Hesperidae all had normal curves with peaks about midday. None of the large day-flying moths, e.g. Burnets, Clearwings or Humming-Bird Hawks was caught, but peak activity in *Ernarmonia succedana* occurred at 14.21 hours (6700 f.c.). In the same genus, the Pea Moth (*E. nigricana* (Fabr.)) also flies in daylight and is most active between 16.00 and 18.00 hours (2700–5000 f.c.) (Wright & Geering, 1947), but the Codling Moth (*E. pomonella* (L.)) flies at dusk (Massee, 1954). Sylvén (1958) studied the flight periodicity of nine fruit-leaf Tortricids in an aktograph. Four species, *Pandemis ribeana* Hüb., *P. heparana* (Schiff.), *Cacoecia podana* Scop. and *C. rosana* L. were most active during the two hours after sunset; four more, *Spilonota ocellana* Schiff., *Argyroplote variegana* Hüb., *Acleris reticulana* Ström. and *Acleris variegana* Schiff. flew after sunset and again before sunrise, and *Cacoecia lechearia* L. flew from noon to sunset but not at night. Edwards (1962) investigated the time of flight of seven species in an aktograph. Males and females of *Ectropis crepuscularia* Schiff. (Geometridae) and *Choristoneura fumiferana* (Clem.) (Tortricidae) flew from before sunset until after sunrise. In contrast *Halisidota argentata* Pack. (Arctiidae), *Nepytia phantasmaria* Stkr. (Geometridae) and *Lambdina somnaria* Hlst. (Geometridae) flew only between sunrise and sunset; *Nepytia* females flew only before midnight, whereas males flew again before dawn. Females of *Anagasta kuhniella* Zell. (Phycitidae) and males of *Malacosma phiviale* Dyar (Lasiocampidae) flew only at sunset, but male *Anagasta* flew more at sunrise than at sunset. Thus only in *Anagasta* and *Nepytia* were there clear differences between the flight times of the sexes.

*Lithocolletis messaniella*, trapped beneath *Quercus ilex* by Crichton (fig. 2, c), was unique among the Lepidoptera in having a bimodal, asymmetrical periodicity curve. During the night peak, approximately 80 per cent. of the moths flying were males, but females predominated in the late afternoon peak (fig. 5, a, b). The explanation for this is unknown.

## COLEOPTERA

Most species of Coleoptera flew in the daytime, particularly during the afternoon, and had a normal shaped periodicity curve. Others flew in the early evening and had curves that were normal or skewed, more commonly away from maximum light than towards it.

The Hydrophilidae and Staphylinidae showed the greatest variety of periodicity curves. The Hydrophilidae gave a sequence of curves, varying from the single normal

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to the asymmetrical bimodal in type. *Cercyon lugubris* had a simple curve with a peak around midday, *C. lateralis*, *C. terminatus*, *C. quisquilius* and *Cryptopleurum minutum* flew from sunrise to sunset. The periodicity curves for *Cercyon atricapillus* and *C. unipunctatus* were bimodal, with the two peaks symmetrically timed in relation to light and greatest in the evening; those for *Helophorus brevipalpis* and *Megasternum obscurum* were also bimodal, but with the two peaks asymmetrically timed. Maximum activity in both occurred once before midday and again just before sunset, but similar numbers of *H. brevipalpis* flew at each time, whereas in *M. obscurum* the midday peak was the greater.

A similar sequence was found in the Staphylinidae. *Oxytelus complanatus*, *Leucoparyphus silphoides*, *O. tetracarinatus* (fig. 6, d) and *O. sculptus* each had single-peaked periodicity curves which, respectively, became progressively later in the afternoon. *Oxytelus tetracarinatus* was one of the few beetles with a curve skewed towards maximum light. *Proteinus ovalis* (fig. 16, j) flew through the day with a sharp peak before sunset, and curves for *Megarthus depressus* (fig. 16, g) and *M. denticollis* (fig. 16, h) were bimodal, with one of the peaks occurring about two hours before sunset.

The Ptiliidae were all daytime flyers, but as species were not determined, the different peaks in the bimodal curves (fig. 12, a) may be due to the presence of more than one species.

*Scydmaenus tarsatus* (Scydmaenidae) flew for a very short time in the late afternoon, at light intensities between 2100 and 3400 f.c., with the curve skewed towards maximum light. In contrast, the spread of the periodicity curves for *Malthinus flaveolus* (Cantharidae) and for *Phyllobius maculicornis* and *P. argentatus* (Curculionidae) (fig. 3, k) was unusually wide, and though most specimens flew in daylight they were occasionally caught in a light intensity as low as that of starlight.

Other weevils (fig. 12, b), Clambidae, Helodidae, Dermestidae, raspberry beetles (Byturidae), pollen beetles (Nitidulidae) (except *Epurea* sp.), Anthicidae, flower beetles (Mordellidae) and flea beetles (Chrysomelidae) (fig. 6, n) were day-flyers. Our mixed species of click beetles (Elateridae) all flew in daylight, but Fryer (1941) remembered netting *Agriotes obscurus* L., *A. lineatus* L. and *A. sputator* L. on a number of occasions between sunset and dark. The Cryptophagidae (fig. 6, f) and Lathridiidae flew in the daytime but were often most active in the afternoon or just before sunset.

Only eight Scarabaeidae, all *Serica brunnea*, were trapped, most of them just after sunset. Many other chafer beetles fly in the evening. *Amphimallon solstitialis* (L.) in Britain (Elton, 1959) and *A. majalis* (Razoumowsky) in New York often swarm around the tops of trees at dusk, the latter when the light intensity is between 13 and 32 f.c. (Evans & Gyrisco, 1958). Young adults of *Melolontha melolontha* L. emerge from the soil and fly at twilight (Schneider, 1952). The garden chafer, *Phyllopertha horticola* (L.) becomes active sometimes between 08.00 and 14.00 hours (Milne, 1958). At the beginning of the flight season, the beetles fly only during one or two hours each day; this period lengthens in the middle of the season, and they may fly until 16.00 hours, but towards the end of the season the duration of daily activity lessens. *Cetonia aurata* (L.), the rose chafer, also flies in bright sunlight.

In Ceylon, females of the Tea Shot-hole borer, *Xyleborus fornicatus* Eichh. (Scolytidae), have a normal flight periodicity curve, with a peak around midday (Calnaido, 1964).

Males of *Elenchus tenuicornis* (Elenchidae, Strepsiptera) were caught occasionally between an hour after sunrise and an hour before sunset (fig. 15, l).

#### HYMENOPTERA

With a few exceptions the Hymenoptera were day-flyers, usually with a normal periodicity curve.

Of the Sawflies (Tenthredinidae), maximum numbers of *Athalia cordata* flew about

noon, but males of *Amauronematus amplus* (fig. 6, g) flew most frequently between 07.00 and 08.00 hours.

Most Braconidae (fig. 3, d), Aphidiidae (fig. 12, f), Ichneumonidae, Pteromalidae Eulophidae (fig. 12, e), Mymaridae (fig. 12, d), Vespidae and Apidae (fig. 1, b) were active in bright light (7000–9000 f.c.) at noon or in the afternoon. Juillet (1960), using rotary traps, showed that Ichneumons, Braconids and Chalcids flew most frequently at high temperatures (20–24° C.). The relatively large Ichneumonids, capable of directed flight, preferred higher humidities than did the smaller Braconids and Chalcids. We caught small numbers of *Ophion* spp. (Ichneumonidae) at night as well as in the day, but too few to allow a periodicity curve to be produced. A few species of Braconidae and Platygasteridae with maximum activity during the afternoon had periodicity curves skewed away from maximum light. The curve for *Vespula rufa* was flat-topped, as would be expected from a local limited population.

The most interesting and unusual periodicity curves in the order occurred in the Cynipidae. Mixed species, including females of *Kleidotoma filicornis*, and *Charips arcuatus* and *Phaenoglyphis salicis*, flew most in the early afternoon, but the sexual and agamic generations of *Neuroterus quercusbaccarum* (fig. 15, j) each flew at different times, the males just before dawn (light intensity 1.2–13.0 f.c.) with small numbers continuing through the day until sunset, whereas the agamic generation reached a peak at 13.20 hours (6,300 f.c.). The explanation is not known. The combined periodicity curve for the species is comparable to that for *Lithocolletis messaniella* (Lep. Gracillariidae) (see p. 425), in that different sexes fly at completely different light intensities and temperatures. It may be significant that both species, the only two out of about 400 caught with this type of curve, are associated with oak. The males in both species fly at a time when they are least likely to be carried away from the host by turbulent air currents.

## DIPTERA

### Nematocera

Day- and night-flyers occurred in most families of Nematocera except the Ptychopteridae (fig. 13, l), Bibionidae (fig. 6, l) and Scatopsidae, which were caught only in daylight. Within families, the day-flyers tended to be darkly pigmented (see p. 416), usually with normal periodicity curves, and the crepuscular- and night-flyers pale, with normal or skew curves. The direction of skewness, towards or away from light, was a family characteristic. In the Tipulidae, Trichoceridae, Culicidae, Bibionidae, Scatopsidae, Mycetophilidae and Cecidomyiidae, skewness was usually towards light, i.e. activity in the evening rapidly reached a maximum and then gradually decreased. In the Anisopidae, Psychodidae, Chironomidae and Ceratopogonidae, skewness was away from maximum light; activity gradually reached a maximum during the evening and then quickly ceased.

Many Nematocera swarm, particularly in the evening, but the characteristics, origins and functions of swarming are referred to elsewhere (Downes, 1955; Frohne, 1959; Gibson, 1945; Haddow & Corbet, 1961; Nielsen & Greve, 1950) and are beyond the scope of this paper.

Most species of Tipulidae reached maximum activity in the two and a half hours after sunset at light intensities of less than 4 f.c. In *Erioptera lutea*, peak activity occurred just before sunset, and *Ormosia nodulosa* flew in the daytime. *Nephrotoma flavescens*, *N. quadrifaria* and *Limonia nubeculosa* had a second peak before sunrise, which was usually much smaller than the evening peak. The *Tipula* sp. (fig. 13, m) was a late flyer, with a peak at 23.06 hours.

Trichoceridae were mainly crepuscular-flyers, flying intermittently in the day. Most individuals of the two species caught, *Trichocera annulata* and *T. regelationis*, flew either before or after sunset, and each species sometimes had a smaller peak at

sunrise. In winter, when light is much dimmer, daytime flight is more common than in summer.

The typical curve for *Anisopus fenestralis* is probably bimodal, with a normal peak at sunset and a smaller one at sunrise (fig. 10, c). This is less obvious from the records of activity in this species (fig. 10, d), collected over sewage beds (Hawkes, 1961), but his data demonstrate that the time of maximum activity moves with change in time of sunset.

The general trend towards normal periodicity curves by day-flyers and skew curves by crepuscular-flyers was reversed with some Psychodidae (fig. 13, e, f). The day-flying species *Pericoma nubila*, *P. fusca* and *Clytocerus ocellaris* all had curves skewed away from maximum light, with peaks in the afternoon. Curves for the crepuscular species were normal, with their maxima around sunset.

Of the Culicidae, *Chaoborus crystallinus* (fig. 13, g) had a normal periodicity curve, with a maximum at 12.36 hours (8000 f.c.). In East Africa, some Chaoborinae also swarm in daylight (Haddow & Corbet, 1961). Most of our other mosquito catches were of *Culex pipiens*; males (fig. 5, h) and immature and gravid females (fig. 5, g) were all most active after sunset at light intensities of 0.048 to 3.6 f.c., and there was usually a small resurgence of activity at dawn. In North America, anopheline mosquitoes are mainly nocturnal (Muirhead-Thomson, 1951); *Anopheles quadrimaculatus* Fay becomes active in the 20 minutes after sunset when the light intensity is falling from 48 to 1 f.c. In South India, *A. annularis* Van der Wulp and *A. culicifacies* Giles swarmed at light intensities between 1.6 and 2.3 f.c. (Rao & Russell, 1938; Russell & Rao, 1942). Provost (1957), using a rotary trap, found that the activity peak in males and females of *Aedes taeniorhynchus* (Wiedemann) occurred at dusk and was most pronounced in males. The biting times of African mosquitoes are well documented but, as Haddow (1954) points out, the relation between flight and feeding is not yet clear.

Maximum activity in the crepuscular Chironomidae (fig. 16, l, m) was precisely defined, with the peak usually slightly earlier than in *Culex*. A few species, e.g. *Tanytarsus subviridis* and *Pentaneura monilis*, had a smaller dawn peak, often with a greater spread than the evening one. Emergence from the pupa follows a daily rhythm in many Chironomids (Morgan & Waddell, 1961; Palmén, 1955; Remmert, 1955a). It frequently coincides with the change in light intensity at dusk and is probably closely associated with the time of flight. *Hydrobaenus foliaceus* (fig. 13, j) flew most in the daytime at light intensities ranging from 2800 f.c. in March to 7600 in August. The light threshold for this species, and for many other day-flyers (fig. 16, k), is thus below 2800 f.c., probably between 1000 and 1500 f.c.

The biting habits of Ceratopogonidae have encouraged interest in their time of flight. We found *Forcipomyia bipunctata* and *Culicoides obsoletus* (fig. 16, e) most active just before sunset at light intensities between 100 and 750 f.c., only a few flying during the day. Reuben, who also used suction traps, found some individuals of *C. impunctatus* (fig. 16, f) flying throughout the day, but most between sunset and midnight (Reuben, 1963). Parker (1949) sampled the air 5 feet above the ground with a net, and detected more females of *Culicoides pallidicornis* Kieffer and of the group of *C. obsoletus* Meigen and more males of *C. pulicaris* (L.) flying around sunset; males of *C. pallidicornis* and females of *C. heliophilus* Edwards were several hours earlier. The time of evening flight relative to sunset was earlier on dark evenings than on light ones. Kettle (1962), using suction traps, confirmed that males of *C. pallidicornis* flew most frequently from one to three hours before sunset, but females did so from sunset until one hour after. He found that *Culicoides grahamii* Austen flew throughout the night but was less abundant after midnight, *Culicoides austeni* Carter, Ingram & Macfie was solely nocturnal, and most individuals of *C. biguttatus* Coquillett flew after midnight. Most species of *Leptoconops* were day-flyers; *L. torrens* (Townsend) emerged in the morning and flew until 10.00 hours, and *L. bequaerta* Kieffer was active all day.

The crepuscular Mycetophilidae, *Mycetophila fungorum* (fig. 13, *d*) and *M. ocellus* (fig. 10, *a*), had mostly bimodal curves but sometimes flew only in the evening. This behaviour also frequently occurred in other families and was probably caused by cool mornings that prevented flight, although light would have permitted it. At dusk, the numbers of Cecidomyiinae flying (fig. 13, *b*) rapidly reached a maximum and diminished gradually through the night; there was no dawn resurgence as in the Mycetophilidae. In these two families, the primitive Sciarinae (fig. 13, *c*) and Lestremiinae (fig. 6, *j*; 13, *a*) were all darkly-pigmented day-flyers.

### *Brachycera*

All the Brachycera caught were active during daylight, most species attaining peak activity in bright light (5000–9000 f.c.), and the distribution was normal (e.g. fig. 3, *f*). *Empis nuntia* (Empididae), *Sciopus platypterus* and *Chrysotus gramineus* (Dolichopodidae) had distinctly bimodal curves, with peaks in the morning and late afternoon, and some Empididae, e.g. *Phylodromia melanocephala* (fig. 3, *j*), had skew curves, with maximum activity in the afternoon. *Rhagio lineola* (Rhagionidae), *P. pallidiventris* (Empididae) and *Microchrysa polita* (Stratiomyidae) all flew for a long time, but *Haematopota pluvialis* (Tabanidae) flew for only a short period in the afternoon. In Uganda, Haddow & Corbet (1961) observed swarms of *Tabanus sulcifrons* about half an hour before sunrise at light intensities between 1 and 5 f.c. and also large numbers of unidentified Stratiomyidae in mid-afternoon.

The Phorid, *Megaselia halterata*, caught in great numbers over mushroom beds, had either a flat-topped periodicity curve or a morning peak.

### *Cyclorrhapha*

The Cyclorrhapha were day-flyers, except for a few crepuscular Acalypterates.

The periodicity curves for different species of Syrphidae were consistently similar. Figure 17, *o* illustrates a generalised curve for the family, and figures 17, *a–n* show the similarity between curves for 13 different species. For all, the curves were normal, most species flying about midday, except for *Metasyrphus consisto* (fig. 17, *l*) and *Syrirta pipiens* (fig. 17, *f*), which flew slightly earlier, between 09.00 and 10.00 hours. Curves for the Dorilaidae were similar to those of Syrphidae.

The Acalypterate families Trypetidae, Sepsidae, Ephydriidae, Agromyzidae and Chloropidae (fig. 1, *a, c*) gave normal curves, commonly with peaks around midday. However, some Acalypterates were characteristically most active at any time during the two and a half hours before sunset (1000–3000 f.c.), often with a critical response to a narrow range of light intensities. The curve for *Tephrochlamys rufiventris* (Helomyzidae) had a standard deviation of only 18 minutes and *Palloptera umbellatarum* (Pallopteridae) flew in the late afternoon for a very limited period. Other species had bimodal curves, with most flight at sunrise and sunset. *Cnemocanthera rorida* (Lauxaniidae) flew for a few hours around sunrise and sunset, and *Opomyza germinationis* had two ill-defined peaks two to three hours after sunrise and before sunset. In contrast, *Drosophila disticha* (fig. 5, *e, f*), *Drosophila graminum* and *Drosophila subobscura* (fig. 5, *c, d*) flew for a short time only, at sunrise and sunset at light intensities of 3–20 f.c., and their periodicity curves at these critical intensities were always skewed away from maximum light. The visual acuity of Drosophilids is discussed elsewhere (p. 404). *Drosophila disticha* and *Thaumatomyia notata* (fig. 10, *g, h*) (Chloropidae), which also had a morning and evening flight in summer, skewed away from light, each having a single normal curve with a peak near to noon on darker, October days. Mitchell & Epling (1951) found that light intensity modified the bimodal periodicity in *Drosophila pseudoobscura*, but that temperature only affected the numbers flying and not the time of flight.

We caught Sphaerocerids only in daylight, but Richards (1930) suggested that some

species fly mainly at night, particularly members of the genus *Trachypella* Duda, which have eyes surprisingly smaller than other members.

Most Cordiluridae, Calliphoridae and Muscidae flew around midday, and their curves were normal (fig. 3, b). The unusually long period over which some Muscids, e.g. *Phaonia rufipalpis* (fig. 1, f), *Pegohylemyia* sp. and *Coenosia sexnotata*, were active is discussed on p. 414.

Sychevskaya (1962) suggests that many Muscidae, and *Calliphora erythrocephala*, have a lower temperature threshold for flight between 5 and 10° C., and an upper threshold between 28 and 37° C., the precise temperature differing according to the species.

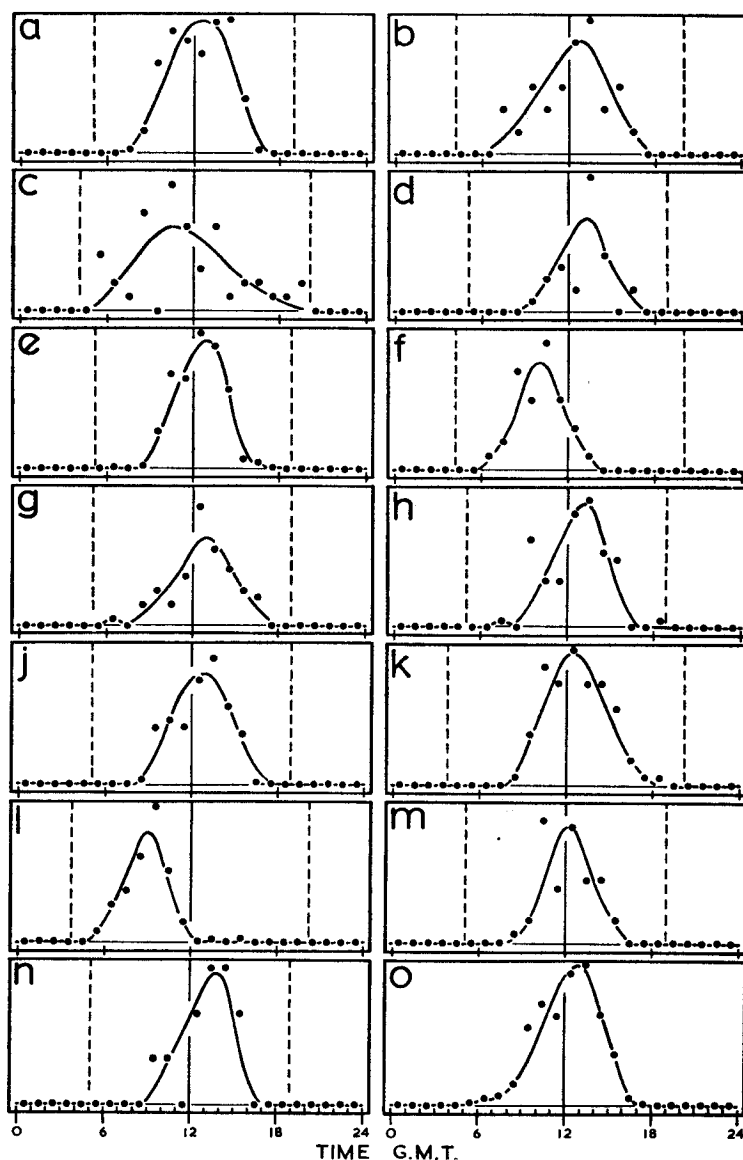


FIG. 17.—Periodicity curves for Syrphidae (Dipt.). The sexes are mixed unless indicated otherwise. (a) *Melanostoma scalare*; (b) *Helophilus* spp., mainly *pendulus*; (c) *Melanostoma mellinum*; (d) *Zelima segnis*; (e) *Episyrphus balteatus*; (f) *Syrpita pipiens*; (g) *Syrphidis vitripennis*; (h) *Rhingia macrocephala*; (j) *Syrphidis ribesii*; (k) *Neoascia podagrica*; (l) *Metasyrphus consisto*, males; (m) *Platycheirus timeo*, males; (n) *Scaeva pyrastris*; (o) total Syrphids.

## XI. SUMMARY

- (1) About five million insects were collected by suction trap from 46 habitats, and the diurnal flight periodicities of 400 taxa, represented by half a million individuals, are described by graphically-fitted probability distributions.
- (2) Different species fly at every hour of the day and night, the duration of flight ranging from half an hour to twenty-four hours.
- (3) The time of flight of males and females differed greatly in only two species.
- (4) Light intensity is the major factor controlling times of flight, which change seasonally with the time of sunrise and sunset.
- (5) Visual acuity at low light intensities is relatively greater in the crepuscular *Drosophila* than in the day-flying *Apis*.
- (6) Predators and flower- and leaf-feeders are mostly day-flyers, finding food by sight. Insects feeding on decaying organic matter and fungi fly mainly in dim light, when sight may be less important than smell and when the air is still and probably helps scent to be detected.
- (7) Time of flight is not related to the size of the insect.
- (8) Small insects, especially Nematocera, predominate in agricultural land, and most pests fly by day.
- (9) High altitude and long distance migration is very highly correlated with flight by day and small size.
- (10) Most insects were caught in temporary habitats, and this suggests that the flight described here is mainly migratory.
- (11) There is a highly significant continuous gradation of colour in the Nematocera, from dark day-flyers to pale night-flyers.
- (12) Night flight has evolved more widely in some orders than in others. It is relatively rare in Coleoptera, Megaloptera, Hymenoptera, Strepsiptera, Cyclorrhapha, Brachycera, Thysanoptera and Hemiptera but predominates in the Neuroptera, Nematocera, Trichoptera and Lepidoptera.
- (13) Data on daily flight periodicity, thought not to be biased by the presence of the traps, are reviewed for each of the orders represented in our catches.

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## APPENDIX A.—Trapping sites

References to further details of trapping sites are indicated by superscript numbers in the last column and are listed in sequence at the end of the Appendix.

SITE NO.	LOCATION AND GRID REF.	SITE	VEGETATION	DATES
1	Valley End Farm, Codicote, Herts. TL198185	Stream	None	31 July–4 Aug. 1963
2	Flatford Mill Field Centre, East Bergholt, Suffolk. TM077333	Stour River-bank	Mixed deciduous woodland Elm. <i>Ulmus</i> sp. Hawthorn. <i>Crataegus monogyna</i> Ing.	14–18 Aug. 1959
3	Millbarn Pond, Oakfield, Reading, Berks. SU672662	Pond	Brambles. <i>Rubus</i> sp. Yew. <i>Taxus bacata</i> L. Oak. <i>Quercus</i> sp. Decaying leaves	23 April–30 July 1963 <sup>1</sup>
4	Rothamsted Experimental Station, Harpenden, Herts. TL124132	Manor Pond	Brambles. <i>Rubus</i> sp. Nettles. <i>Urtica dioica</i> L.	28 June–18 July 1962
5	Birmingham, Tame & Rea District Drainage Board, Rookery Park, Erdington, Birmingham 24. SP166923	Filter Beds	None	1 April 1956–31 Oct. 1957 <sup>2</sup>
6	Rothamsted Experimental Station, Harpenden, Herts. TL132136	Compost Heap	Rotting Compost	17–20 July 1962, 15–17 Oct. 1962
7	Culberry Nursery, Angmering, Sussex. TQ074052	Mushroom Beds	Mushrooms. <i>Psalliota hortensis</i>	12 Aug.–16 Sept. 1963 <sup>3</sup>
8	Lephinmore, Loch Fyne, Argyllshire. NR985930	Moorland field	Rough pasture, grass White clover. <i>Trifolium repens</i> L.	20 June–21 Sept. 1957, <sup>4</sup> 2–20 Aug. 1958
9	Flatford Mill Field Centre, East Bergholt, Suffolk. TM077333	Salt Marsh	<i>Glyceria</i> sp. Reeds. <i>Phragmites</i> sp.	11–18 Aug. 1962
10	TM077333	Ditch	Sedges. <i>Carex</i> sp.	14–21 Aug. 1963
11	Rothamsted Experimental Station, Harpenden, Herts. TL123132	Manor Moat (dry)	Nettles. <i>U. dioica</i> L. Bracken. <i>Pteridium aquilinum</i> (L.) Grass	14–25 June 1962
12	TL124133	Manor Garden	Knappweed. <i>Centaurea nigra</i> L.	11–17 July 1963
13	R. and D.E., Ministry of Aviation, Cardington, Beds. TL08154640	Airfield	Coarse Pasture	24 Sept.–21 Oct. 1953, <sup>5</sup> 25 July–28 Oct. 1954, 21 July–18 Oct. 1955
14	Rothamsted Experimental Station, Harpenden, Herts. TL132133	Lawn	Mixed Grasses	8 June–25 Oct. 1962 <sup>6</sup>
15	TL129133	Great Field II	Oats. <i>Avena sativa</i> L.	1–30 June, 10–14 July 1960, 26, 29, 30, 31 Aug. 1960, 1 June–15 July 1961 <sup>7</sup>
16	Entomological Field Station, Storeys Way, Cambridge. TL433596	Field	Oats. <i>A. sativa</i> L.	15 July–3 Aug. 1960
17	Silwood Park Field Station, Sunninghill, nr. Ascot, Berks. SU944688	Field	Wheat. <i>Triticum aestivum</i> L.	22 July–12 Aug. 1957, 5 June–18 July 1958 <sup>8</sup>
18	Muguga, Kikuya, Kenya. 1.0° S. 36.20° E.	Wattle forest clearing	<i>Pyrethrum</i> sp.	Jan. 1953–Jan. 1955 <sup>9</sup>
19	Rothamsted Experimental Station, Harpenden, Herts. TL133136	West Building Allotments	Kale. <i>Brassica oleracea</i> L.	9 Aug.–30 Nov. 1961, <sup>10</sup> 29 Aug.–12 Oct. 1962
20	TL129132	Great Field I	Field Beans. <i>Vicia faba</i> L.	10–31 July 1948 <sup>11</sup>
21	Rothamsted Lodge, Harpenden, Herts. TL133131	Walled Garden	Field Beans. <i>V. faba</i> L.	2–26 July 1952, <sup>12</sup> 23 June–28 July 1949, <sup>13</sup> 5 July–2 Aug. 1949 <sup>14</sup>
			Bare plot	23–29 Sept. 1949

## APPENDIX A.—continued

SITE No.	LOCATION AND GRID REF.	SITE	VEGETATION	DATES
22	Rothamsted Experimental Station, Harpenden, Herts. TL134136	Allotments	Potatoes. <i>Solanum tuberosum</i>	25 June–28 July 1949 <sup>15</sup>
23	TL132135	Copse	Nettles. <i>U. dioica</i>	8 June 1962
24	TL132136	Cesspit	Nettles. <i>U. dioica</i>	22 May–13 June 1962, 16–18 Oct. 1962, 17–29 July 1963
25	Pré Mill, Gorhambury, St. Albans, Herts. TL128086	Stream	Nettles. <i>U. dioica</i>	9–17 Oct. 1962
26	TL127085	Stream	Willowherb. <i>Epilobium hirsutum</i> L. Nettles. <i>U. dioica</i>	24–31 July 1963
27	Cress Farm, Redbournbury, Herts. TL120109	Cress Beds	Comfrey. <i>Symphytum officinale</i> L. Watercress. <i>Nasturtium officinale</i> R.Br.	27 June–2 July 1963
28	Rothamsted Experimental Station, Harpenden, Herts. TL125132	Manor Garden	<i>Spiraea</i> sp.	21–29 July 1962, 12–17 July 1963
29	Coldharbour Farm, Aldbury, Tring, Herts. SP986114	Heathland	Gorse. <i>Ulex europaeus</i> L. Brambles. <i>Rubus</i> sp. Knapweed. <i>Centaurea</i> sp. Grass.	26 April–8 June 1963, 10 July–5 Sept. 1963
30	St. Ives Sand & Gravel Co. Ltd. Codicote, Herts. TL211182	Quarry face	Broom. <i>Cytisus scoparius</i> L.	31 July–4 Aug. 1963
31	Flatford Mill Field Centre, East Bergholt, Suffolk. TM077333	Willy Lott's meadow	Broom. <i>C. scoparius</i> L.	14–21 Aug. 1963
32	Rivers Lodge, Harpenden, Herts. TL135135	Walled Garden	Spindle bushes. <i>Euonymus europaeus</i>	31 May–3 June 1957
33	Rothamsted Experimental Station, Harpenden, Herts. TL136132	Manor Wood	<i>Rhododendron</i> sp.	28 Oct.–1 Nov. 1962
34	TL122130	Manor Garden	<i>Rhododendron</i> sp.	7–12 June 1962
35	TL122130	Manor Garden	<i>Rhododendron</i> sp.	14 Sept.–5 Oct. 1962
36	TL123129	Manor Wood	<i>Rhododendron</i> sp.	24 Oct.–2 Nov. 1962
37	TL123133	Manor Orchard	<i>Rhododendron</i> sp. Apple. <i>Pyrus malus</i>	31 July–8 Aug. 1962, 14 Sept.–3 Oct. 1962, 28 Oct. 1953
38	Millbarn Pond, Oakfield, Reading, Berks. SU672662	Garden	Holme Oak. <i>Quercus ilex</i> L.	5 Oct.–11 Nov. 1963 <sup>16</sup>
39	Rothamsted Experimental Station, Harpenden, Herts. TL122130	Manor Garden	Oak Canopy. <i>Quercus</i> sp.	24 May–18 June 1962
40	TL124132	Manor Garden	Beech Canopy. <i>Fagus sylvatica</i> L.	18–25 June 1962
41	TL132135	Great Field IV	Elm Canopy. <i>Ulmus</i> sp.	25 June–10 July 1962
42	Entomological Field Station, Storeys Way, Cambridge. TL433596	Garden	Austrian Pines. <i>Pinus laricio</i> var. <i>nigricans</i> Parl.	22–27 March 1961 <sup>17</sup>
43	Flatford Mill Field Centre, East Bergholt, Suffolk. TM077333	Copse	Elm. <i>Ulmus</i> sp. Nettles. <i>U. dioica</i>	10–17 Aug. 1960
44	Rothamsted Experimental Station, Harpenden, Herts. TL125131	Manor Wood	Celandine. <i>Ranunculus ficaria</i> L. Nettles. <i>U. dioica</i> Oaks. <i>Quercus</i> sp.	23 Jan.–19 May 1962
45	Thunderdell Lodge, Ringshall Road, Little Gaddesdon, Herts. SP979125	Woodland	Beech. <i>F. sylvatica</i> Silver Birch. <i>Betula verrucosa</i> Ehoh. Brambles. <i>Rubus</i> sp. Bracken. <i>P. aquilinum</i>	26 April–10 July 1963
46	Rothamsted Experimental Station, Harpenden, Herts. TL129133	Great Field II	Oat Stubble. <i>A. sativa</i>	20–23 Sept. 1960

## APPENDIX A.—continued

Note.—All grid references are taken from the seventh series of 1 inch Ordnance Survey maps, except Site 13, which was taken from a 6 inch O.S. map, and Site 18, the latitude and longitude of which were obtained from the *Times Atlas*.

- <sup>1</sup> Crichton, M. I. (1960).
- <sup>2</sup> Hawkes, H. A. (1961).
- <sup>3</sup> Hussey, N. W. (*unpubl.*).
- <sup>4</sup> Reuben, R. (1963).
- <sup>5</sup> Taylor, L. R. & Carter, C. I. (1961).
- <sup>6</sup> Calnaido, D., French, R. A. & Taylor, L. R. (1964).
- <sup>7</sup> French, R. A. & Smith, F. M. (*unpubl.*).
- <sup>8</sup> Lewis, T. (1959).
- <sup>9</sup> Eastop, V. F. (1957).
- <sup>10</sup> El Khidir, E. (1963).
- <sup>11</sup> Johnson, C. G. (1950b).
- <sup>12</sup> Johnson, C. G., Taylor, L. R. & Haine, E. (1957).
- <sup>13</sup> Eastop, V. F. (1951); Johnson, C. G. (1952).
- <sup>14</sup> Banks, C. J. (1952).
- <sup>15</sup> Eastop, V. F. (1951); Johnson, C. G. (1952).
- <sup>16</sup> Crichton, M. I. (*unpubl.*).
- <sup>17</sup> Lewis, T. (1963).

## APPENDIX B.—Catalogue of flight periodicities

Species are arranged in taxonomic order after Kloet & Hincks (1945). Where the nomenclature has been revised in preparation for a second edition of this *Check List*, the new name is also given in square brackets. Species not listed in Kloet & Hincks are marked with an asterisk.

When the time of flight each day is represented by a simple curve, there is one mean time of flight with a standard deviation (S.D.) (col. 6). When there are two peaks of flight, the time of each peak has its own mean and S.D., but the insects flying may be variously distributed between these two peaks. The proportions (percentage) flying in each peak are thus referred to in column 5 as the "Percentage population represented". For populations with a single peak of flight activity, this is always 100 per cent. Curve shapes are designated as S., .S, or N.

S. means that the curve is skewed towards maximum light, *i.e.* the mode is nearer to noon than the mean.

.S means that the curve is skewed away from maximum light, *i.e.* the mean is nearer to noon than the mode.

N means that the curve is not skewed.

Figures quoted after families indicate where periodicity curves for species from the family are illustrated.

The sex of the individuals is specified where known.

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<b>PSOCOPTERA</b>							
STENOPSOCIDAE fig. 12							
<i>Stenopsocus immaculatus</i> (Stephens)	33	Oct., Nov. 1962	150	100	08·10 (240)	1100	2 (.S)
CAECILIIDAE							
<i>Trichopsocus dalii</i> (McLachlan)	33	Oct., Nov. 1962	36	53	06·50 (150)	0·0013	34 (N)
				47	12·45 (78)		
<i>Lachesilla pedicularia</i> (L.)	21	Sept. 1949	437	100	14·00 (95)	7600	6 (N)
PERIPSOCIDAE							
<i>Ectopsocus briggsi</i> (McLachlan)	2 Aug. 1959 } 43 Aug. 1960 }		116	68	13·12 (329)	3000	42 (N)
				32	19·00 (55)		
<b>EPHEMEROPTERA</b>							
EPHEMERELLIDAE fig. 15							
<i>Ephemerella ignita</i> (Poda) ♀	1	July, Aug. 1963	64	100	19·30 (30)	70	14 (N)
<b>ODONATA</b>							
COENAGRIIDAE fig. 15							
<i>Ischnura elegans</i> (van der Linden) ♂	3	June, July 1963	20	100	11·52 (101)	9500	6 (N)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<b>THYSANOPTERA</b>							
<b>AEOLOTHRIPIDAE</b>							
<i>Aeolothrips fasciatus</i> (L.)	}	17 July, Aug. 1957	33	100	12.00 (116)	9200	6 (N)
<i>Aeolothrips tenuicornis</i> Bagnall		21 July 1952	200	100	12.38 (152)	9000	6 (N)
<i>Aeolothrips fasciatus</i> (L.)		}	16 July, Aug. 1960	274	100	12.16 (154)	9200
<i>Aeolothrips tenuicornis</i> Bagnall							
<i>Aeolothrips fasciatus</i> (L.)							
<i>Aeolothrips tenuicornis</i> Bagnall							
<b>THRIPIDAE figs. 3, 12</b>							
<i>Limothrips cerealium</i> Haliday ♀		16 July, Aug. 1960	9605	100	12.06 (150)	9200	6 (N)
„ „ „ ♀		17 June, July 1958	4205	100	12.48 (126)	9000	6 (N)
„ „ „ ♀		17 July, Aug. 1957	16,880	100	11.54 (147)	9000	6 (N)
„ „ „ ♀		21 July 1952	1036	100	12.20 (156)	9000	6 (N)
<i>Limothrips cerealium</i> Haliday ♀	}	15 June 1960	3324	100	12.22 (157)	9500	6 (N)
<i>Limothrips denticornis</i> Haliday ♀							
<i>Stenothrips graminum</i> Uzel mixed		2 Aug. 1959	712	100	14.42 (160)	6300	13 (S)
„		44 April 1962	820	100	13.24 (128)	6300	6 (N)
<b>PHLAEOTHRIPIDAE fig. 12</b>							
<i>Phlaeothrips coriaceus</i> Haliday [ <i>Euphlaeothrips coriaceus</i> (Haliday)]	44	April 1962	73	100	14.12 (114)	5100	12 (N)
<b>HEMIPTERA</b>							
<b>ANTHOCORIDAE fig. 16</b>							
<i>Anthocoris nemorum</i> (L.)	28	July 1962	101	100	12.26 (138)	9000	6 (N)
<i>Orius niger</i> (Wolff)	28	July 1962	189	100	13.48 (134)	8000	6 (N)
<i>Orius minutus</i> (L.) mainly	21	July 1952	671	100	13.44 (209)	8000	6 (N)
<i>Orius</i> sp.	2	Aug. 1959	40	100	13.02 (130)	7600	6 (N)
<b>MIRIDAE fig. 16</b>							
<i>Systratius nigruta</i> (Fallén) [ <i>Polymerus nigrutus</i> (Fallén)]	26	July 1963	13	100	12.17 (159)	9000	6 (N)
<i>Monalocoris filicis</i> (L.)	11	June 1962	24	100	12.55 (115)	9500	6 (N)
„ „ „	45	May 1963	40	100	13.39 (136)	7800	6 (N)
<i>Dicyphus epilobii</i> Reuter	26	July 1963	186	100	14.54 (153)	7000	12 (N)
<i>Orthotylus virescens</i> (Douglas & Scott)	30	July, Aug. 1963	79	28	19.00 (145)		28 (N)
				72	05.08 (105)	630	

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/ candles)	Curve type (shape shown in brackets)
<i>HEMIPTERA (contd.)</i>							
TETTIGONIIDAE fig. 15							
<i>Graphocephala coccinea</i> (Forster)	35	Sept., Oct. 1962	34	100	12·35 (123)	6200	6 (N)
BYTHOSCOPIIDAE							
<i>Oncopsis flavicollis</i> (L.) ♀	45	June, July 1963	13	60	10·55 (320)	8000	42 (N)
				40	17·30 (86)		
„ „ „ ♂	45	June 1963	216	25	11·45 (330)		40 (N)
				75	18·24 (94)	2100	
JASSIDAE fig. 15							
<i>Eupelix cuspidata</i> (Fabr.)	29	July, Aug. 1963	14	100	11·43 (67)	8800	5 (N)
<i>Deltocephalus flori</i> Fieber [ <i>Jassargus flori</i> (Fieber)]	29	July, Aug. 1963	18	100	14·52 (120)	6000	13 (S)
<i>Macrosteles sexnotatus</i> (Fallén)	15	June 1960	344	30	06·38 (74)		29 (N)
				70	19·20 (75)	1000	
TYPHLOCYBIDAE							
<i>Typhlocyba ulmi</i> (L.)	41	June, July 1962	546	40	05·04 (100)		41 (N)
				60	11·20 (244)	2400	
<i>Typhlocyba cruciata</i> Ribaut	24	Oct. 1962	47	100	14·17 (146)	2500	13 (S)
<i>Typhlocyba prunicola</i> Edwards	24	July 1963	49	50	10·36 (382)		41 (N)
				50	17·18 (103)	2700	
<i>Cicadella urticae</i> (Fabr.)	24	Oct. 1962	206	100	12·13 (120)	4800	6 (N)
<i>Cicadella aurata</i> (L.) [ <i>Eupteryx aurata</i> (L.)]	24	July 1963	314	24	06·04 (221)		37 (N)
				76	15·48 (120)	5600	
<i>Empoasca flavescens</i> (Fabr.)	35	Sept., Oct. 1962	198	56	11·33 (206)	1700	41 (N)
				44	16·36 (94)		
<i>Dikraneura variata</i> Hardy	45	May 1963	19	100	12·51 (219)	8500	6 (N)
CHERMIDAE fig. 12							
<i>Trioza urticae</i> (L.)	24	Oct. 1962	35	100	13·00 (76)	3700	5 (N)
„ „ „	24	July 1963	23	100	12·36 (103)	9000	6 (N)



## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D.) (in mins.) shown in brackets	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<i>HEMIPTERA (contd.)</i>							
ALEYRODIDAE figs. 2, 5, 10							
<i>Aleyrodes proletella</i> (L.)	19	Sept., Oct. 1962	2853	100	12·48 (104)	6000	6 (N)
„ „ „ ♀	19	Aug., Sept. 1961	15,825	100	13·18 (141)	7500	6 (N)
„ „ „ ♂	19	Aug., Sept. 1961	3394	100	12·51 (163)	8000	6 (N)
„ „ „ ♂	19	Sept., Oct. 1961	672	100	11·03 (208)	5000	6 (N)
„ „ „ ♀	19	Sept., Oct. 1961	20,437	71	11·30 (126)	6300	27 (N)
				29	23·57 (207)		
APHIDIDAE figs. 1, 2, 12							
<i>Macrosiphum euphorbiae</i> (Thomas)	21	June–Aug. 1949	36	48	08·39 (125)		23 (N)
				52	16·15 (125)	4400	
<i>Macrosiphum rosae</i> (L.)	21	June, July 1949	86	12	08·42 (107)		29 (N)
				88	18·03 (78)	3450	
<i>Macrosiphum avenae</i> (Fabr.)	21	June–Aug. 1949	41	35	08·39 (120)		29 (N)
				65	17·24 (104)	2675	
<i>Macrosiphum</i> spp.	18	June–Aug. 1953	25	100	16·45 (517)	3600	12 (N)
<i>Acyrtosiphon onobrychidis</i> (Fonscolombe)	18	June–Aug. 1953	74	100	14·48 (199)	6600	12 (N)
[ <i>Acyrtosiphon pisum</i> (Harris)]	21	June, July 1949	41	33	08·57 (136)		29 (N)
„ „ „				67	16·05 (94)	5100	
<i>Acyrtosiphon carnosum</i> (Buckton)	32	May, June 1957	9131	75	16·54 (72)	3550	37 (N)
				25	10·32 (100)		
<i>Dactynotus jaceae</i> (L.)	21	June, July 1949	248	24	09·02 (105)		37 (N)
				76	17·38 (82)	2800	
* <i>Dactynotus compositae</i> (Theobald)	18	June–Aug. 1953	31	100	14·04 (217)	7600	12 (N)
<i>Nasonovia ribicola</i> (Kaltenbach)	21	June, July 1949	28	100	13·20 (262)	8600	6 (N)
[ <i>Nasonovia ribisnigri</i> (Mosley)]	21	June, July 1949	227	50	09·28 (116)	7400	23 (N)
<i>Hyperomyzus lactucae</i> (L.)				50	15·44 (118)		
<i>Myzus persicae</i> (Sulzer)	18	June–Aug. 1953	55	100	14·40 (276)	6700	13 (S)
„ „ „	21	June, July 1949	79	100	13·36 (304)	8400	8 (S)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<i>HEMIPTERA (contd.)</i>							
<i>APHIDIDA</i> figs. 1, 2, 12 (contd.)							
* <i>Lipaphis pseudobrassicae</i> (Davis)	18	June–Aug. 1953	119	100	13·58 (344)	7700	6 (N)
<i>Cavariella aegopodii</i> (Scopoli)	21	June, July 1949	440	40	12·00 (242)		41 (N)
				60	17·30 (80)	6800	
<i>Cavariella umbellatarum</i> (Koch) [ <i>Cavariella theobaldi</i> (Gillette & Bragg)]	21	June, July 1949	44	100	17·08 (178)	3550	12 (N)
<i>Semiaphis atriplicis</i> (L.) [ <i>Hayhurstia atriplicis</i> (L.)]	21	June–Aug. 1949	41	68	11·30 (170)	9000	36 (N)
				32	17·40 (40)		
<i>Hyalopterus arundinis</i> (Fabr.) [ <i>Hyalopterus pruni</i> (Geoffroy)]	21	June, July 1949	585	22	09·37 (136)		29 (N)
				78	16·24 (142)	4700	
<i>Rhopalosiphum foeniculi</i> (Passerini) [ <i>Hyadaphis foeniculi</i> (Passerini)]	21	June, July 1949	54	100	14·27 (166)	7500	12 (N)
* <i>Rhopalosiphum rufiabdominalis</i> (Sasaki)	18	June–Aug. 1953	31	100	13·12 (241)	8400	6 (N)
* <i>Rhopalosiphum maidis</i> (Fitch) ♀	18	June–Aug. 1953	283	100	14·48 (277)	6800	12 (N)
<i>Doralis fabae</i> (Scopoli) [ <i>Aphis fabae</i> (Scopoli)]	20	July 1948	1519	46	11·00 (157)		41 (N)
				54	16·08 (190)	7000	
“ “ “	22	July 1949	3881	40	10·30 (102)		34 (N)
				60	17·30 (150)	2700	
“ “ “	21	June, July 1949	21,240	50	10·30 (120)	9000	41 (N)
				50	15·30 (180)		
“ “ “	21	July 1952	22,119	100	11·36 (276)	9000	6 (N)
<i>Aphis</i> spp.	18	June–Aug. 1953	158	100	14·20 (375)	8200	12 (N)
<i>Brachycaudus helichrysi</i> (Kaltenbach)	21	June–Aug. 1949	60	100	15·44 (141)	5300	12 (N)
<i>Brachycaudus rumexicolens</i> (Patch) [ <i>Thuleaphis rumexicolens</i> (Patch)]	21	June, July 1949	50	20	09·30 (140)		29 (N)
				80	15·16 (127)	6000	
<i>Myzocallis coryli</i> (Goeze)	21	June, July 1949	359	26	08·45 (168)		29 (N)
				74	16·03 (144)	5300	
<i>Myzocallis castanicola</i> Baker	21	June, July 1949	84	100	16·28 (162)	4600	13 (S)
<i>Myzocallis annulatus</i> (Hartig) [ <i>Tuberculoides annulatus</i> (Hartig)]	21	June, July 1949	121	100	12·31 (342)	9400	8 (S)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/ candles)	Curve type (shape shown in brackets)
<b>HEMIPTERA (contd.)</b>							
<b>APHIDIDAE (contd.)</b>							
<i>Myzocallis tiliae</i> (L.) [ <i>Eucallipterus tiliae</i> (L.)]	21	June, July 1949	90	100	13·16 (220)	8650	8 (S)
<i>Anoecia corni</i> (Fabr.)	21	June, July 1949	43	100	13·27 (180)	8600	8 (S)
<i>Eriosoma ulmi</i> (L.) [ <i>Schizoneura ulmi</i> (L.)]	21	June, July 1949	219	50	12·04 (220)		41 (N)
				50	16·54 (120)	7500	
mixed aphids	18	June–Aug. 1953	68	100	14·05 (299)	7600	13 (S)
“ “	3	June, July 1963	1145	100	13·44 (210)	8300	6 (N)
“ “	32	May, June 1957	9989	40	10·49 (109)		34 (N)
				60	16·40 (117)	3850	
“ “	15	June 1960	1849	60	11·48 (188)	7800	41 (N)
				40	16·54 (108)		
<b>MEGALOPTERA</b>							
<b>SIALIDAE fig. 15</b>							
<i>Sialis lutaria</i> (L.)	3	May, June 1963	31	100	11·28 (133)	9000	8 (S)
<b>NEUROPTERA</b>							
<b>CONIOPTERYGIDAE fig. 15</b>							
<i>Conwentzia psociformis</i> (Curtis)	39 & 34	June 1962	97	50	21·42 (86)	0·13	24 (S)
				50	01·24 (94)		
<b>SISYRIDAE fig. 15</b>							
<i>Sisyra fuscata</i> (Fabr.)	3	June, July 1963	88	30	07·02 (123)		37 (N)
				70	19·36 (72)	630	
<b>HEMEROBIIDAE fig. 10</b>							
<i>Eumicromus paganus</i> (L.) [ <i>Micromus paganus</i> (L.)]	11	June 1962	45	100	21·50 (90)	0·13	15 (S)
<i>Kimminsia subnebulosa</i> (Stephens)	21	July, Aug. 1949	113	100	22·12 (88)	0·0008	15 (S)
“ “ “	19	Sept., Oct. 1961	35	100	21·10 (74)	0·00008	15 (S)
<b>CHRYSOPIIDAE</b>							
<i>Chrysopa carnea</i> Stephens	44	May 1962	76	50	22·24 (135)		26 (N)
				50	02·36 (158)	0·4	
“ “ “	38	Oct. 1963	28	100	23·03 (328)	0·00008	21 (N)
<b>TRICHOPTERA</b>							
<b>POLYCENTROPIDAE fig. 15</b>							
<i>Cyrnus trimaculatus</i> (Curtis)	3	June, July 1963	42	100	16·36 (60)	4350	9 (N)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins. shown in brackets))	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<b>TRICHOPTERA (contd.)</b>							
PSYCHOMYIIDAE fig. 15							
<i>Ecnomus tenellus</i> (Rambur)	3	June, July 1963	23	100	19.42 (117)	500	19 (S)
HYDROPTILIDAE fig. 15							
<i>Orthotrichia tetensii</i> Kolbe	3	June, July 1963	26	30	10.19 (89)		37 (N)
				70	17.12 (22)	3450	
<b>LEPIDOPTERA</b>							
CARADRINIDAE fig. 6							
<i>Amphipyra tragopogonis</i> (L.)	13	Sept., Oct. 1954 } Sept., Oct. 1955 }	234	85	20.03 (71)	0.00008	40 (N)
				15	02.28 (88)		
<i>Caradrina morpheus</i> (Hufnagel)	27	June, July 1963	28	100	22.46 (69)	0.0035	20 (N)
<i>Xylophasia monoglypha</i> (Hufnagel) [ <i>Apamea monoglypha</i> (Hufnagel)]	13	July 1954 } Aug. 1955 }	17	53	21.32 (100)	0.0052	23 (N)
				47	02.28 (104)		
<i>Celaena secalis</i> (L.) [ <i>Apamea secalis</i> (L.)]	29	July, Aug. 1963	11	100	02.09 (59)	0.002	1 (S.)
" " "	29	July, Aug. 1963	14	21	20.30 (50)		41 (N)
	26	July 1963					
	31	Aug. 1963		79	03.10 (42)	0.06	
	1	July, Aug. 1963					
	24	July 1963					
	12	July 1963					
<i>Euxoa nigricans</i> (L.)	13	July 1955	30	100	21.19 (58)	0.048	20 (N)
<i>Triphaena pronuba</i> (L.) [ <i>Noctua pronuba</i> (L.)]	13	Aug., Sept. 1954 } Aug., Sept. 1955 }	18	100	21.05 (127)	0.0004	18 (S.)
<i>Phalaena typica</i> L. [ <i>Naenia typica</i> (L.)]	29	July, Aug. 1963	10	100	23.48 (66)	0.00025	20 (N)
<i>Agrochola lychnidis</i> (Schiffermueller)	13	Oct. 1953 } Oct. 1954 } Oct. 1955 }	165	100	17.53 (65)	0.95	16 (S)
<i>Leucania impura</i> (Hübner)	29	July, Aug. 1963	13	100	21.36 (45)	0.005	14 (N)
	12	July 1963					
	24	July 1963					
PLUSIIDAE fig. 6							
<i>Hypena proboscidalis</i> (L.)	27	June, July 1963	38	100	21.29 (114)	0.08	18 (S.)
" " "	26	July 1963	82	100	22.16 (110)	0.0033	18 (S.)
	12	July 1963					
	24	July 1963					
<i>Plusia chrysitis</i> (L.)	27	June, July 1963	78	100	22.23 (139)	0.0085	18 (S.)
<i>Plusia gamma</i> (L.)	29	Aug. 1963	48	55	19.57 (81)	8.0	25 (S.)
				45	03.37 (126)		

## APPENDIX B.—continued

APPENDIX B.—*continued*

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<b>LEPIDOPTERA (contd.)</b>							
<b>STERRHIDAE</b>							
<i>Sterrha dimidiata</i> (Hufnagel)	29	July 1963	76	100	01·12 (99)	0·0033	22 (N)
	26	July 1963					
	1	July, Aug. 1963					
	12	July 1963					
	24	July 1963					
<b>HYDRIOMENIDAE</b>							
<i>Lygris dotata</i> (L.)	27	June, July 1963	21	100	22·24 (60)	0·0085	20 (N)
[ <i>Lygris pyraliata</i> (Denis & Schiffermueller)]							
<i>Xanthorhoe montanata</i> (Schiffermueller)	11	June 1962	23	100	23·36 (132)	0·0014	21 (S.)
<i>Calostigia pectinataria</i> (Knoch)	29	July 1963	20	100	22·27 (119)	0·0033	22 (N)
	27	July 1963					
	26	July 1963					
<b>NYMPHALIDAE fig. 3</b>							
<i>Nymphalis io</i> (L.)	29	Aug. 1963	21	100	12·16 (75)	8500	5 (N)
<b>PIERIDAE</b>							
<i>Pieris brassicae</i> (L.)	29	Aug. 1963	17	100	12·12 (104)	8500	6 (N)
<i>Pieris rapae</i> (L.)	29	Aug. 1963	33	100	11·54 (119)	8500	6 (N)
<i>Pieris napi</i> (L.)	29	Aug. 1963	21	100	12·13 (125)	8500	6 (N)
<b>HESPERIIDAE</b>							
<i>Thymelicus sylvestris</i> (Poda)	29	July, Aug. 1963	12	100	12·30 (148)	8800	6 (N)
	26	July 1963					
<b>CRAMBIDAE fig. 6</b>							
<i>Crambus culmellus</i> (L.)	14	Aug. 1962	274	100	20·54 (84)	0·023	15 (S.)
[ <i>Agriphila straminella</i> (Denis & Schiffermueller)]							
<i>Crambus culmellus</i> (L.)	14	July 1962	166	100	21·42 (94)	0·048	19 (S.)
<i>Crambus hortuellus</i> (Hübner)	14	July 1962	231	100	00·18 (128)	0·0033	22 (N)
[ <i>Amphibolia culmella</i> L.]							
<i>Crambus perlellus</i> (Scopoli)	14	July 1962	189	100	23·42 (99)	0·00046	22 (N)
<b>PYRAUSTIDAE</b>							
<i>Phlyctaenia lutealis</i> (Hübner)	29	July, Aug. 1963	18	100	00·15 (91)	0·0006	21 (S.)
[ <i>Udea lutealis</i> Hübner]	24	July 1963					
<i>Scoparia ambigualis</i> (Treitschke)	29	July 1963	44	100	21·24 (86)	0·048	15 (S.)
	12	July 1963					
	24	July 1963					
<b>ALUCITIDAE fig. 6</b>							
<i>Platyptilia pallidactyla</i> (Haworth)	29	July 1963	81	100	21·00 (75)	0·048	17 (N)
<b>TORTRICIDAE fig. 6</b>							
<i>Pandemis heparana</i> (Schiffermueller)	37	Sept., Oct. 1962	18	100	20·36 (22)	0·00008	20 (N)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<b>LEPIDOPTERA (contd.)</b>							
<b>TORTRICIDAE fig. 6 (contd.)</b>							
<i>Tortrix viridana</i> (L.)	3	June, 1963	33	43	01·36 (39)		23 (N)
				57	20·50 (66)	0·01	
<i>Tortrix costana</i> Schiffermueller	26	July 1963	148	100	23·32 (31)	0·00046	20 (N)
[ <i>Clepsis costana</i> (Schiffermueller)]	27	June, July 1963	94	100	23·03 (64)	0·002	20 (N)
<b>EUCOSMIDAE fig. 6</b>							
<i>Eucosma cana</i> (Haworth)	29	July 1963	102	100	20·50 (61)	3·6	14 (N)
	26	July 1963					
	12	July 1963					
	24	July 1963					
<i>Argyroplote nubiferana</i> (Haworth)	29	July 1963	10	100	23·40 (78)	0·00046	20 (N)
[ <i>Hedya nubiferana</i> (Haworth)]	12	July 1963					
	24	July 1963					
<i>Argyroplote lacunana</i> (Schiffermueller)	29	July 1963	294	20	20·15 (100)		32 (S.)
	26	July 1963					
	12	July 1963					
[ <i>Olethreutes lacunana</i> (Schiffermueller)]	24	July 1963		80	01·30 (108)	0·0033	
<i>Ernarmonia succedana</i> (Schiffermueller)	29	May 1963	262	100	14·21 (149)	6700	12 (N)
[ <i>Laspeyresia succedana</i> Schiffermueller]							
<b>OECOPHORIDAE</b>							
<i>Carcina quercana</i> (Fabr.)	35	Sept., Oct. 1962	20	100	20·51 (75)	0·00008	18 (S.)
<b>GLYPHIPTERIGIDAE</b>							
<i>Glyphipterix cramerella</i> (Fabr.)	24	May, June 1962	190	100	14·18 (130)	7500	13 (S.)
<b>ELACHISTIDAE</b>							
<i>Elachista cerusella</i> (Huebner)	9	Aug. 1962	113	100	19·48 (46)	8·0	15 (S.)
<b>COLEOPHORIDAE</b>							
<i>Coleophora albicosta</i> (Haworth)	29	May 1963	322	30	20·20 (114)		28 (N)
				70	02·54 (35)	0·0074	
<b>GRACILLARIIDAE figs. 2, 5</b>							
<i>Lithocolletis messaniella</i> Zeller	38	Oct., Nov. 1963	10,275	47	15·39 (202)		34 (N)
				53	03·22 (149)	0·00008	
" " " ♂	38	Oct. 1963	981	16	16·24 (130)		36 (N)
				84	04·09 (156)	0·00008	
" " " ♀	38	Oct. 1963	1158	73	17·30 (198)	0·95	29 (N)
				27	03·54 (140)		

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/ candles)	Curve type (shape shown in brackets)
<i>LEPIDOPTERA (contd.)</i>							
<i>PLUTELLIDAE</i>							
<i>Plutella maculipennis</i> (Curtis)	14	July 1962	117	100	22·07 (166)	0·0033	18 (S.)
„ „ „	14	Aug. 1962	24	100	21·34 (191)	0·00058	18 (S.)
„ „ „	14	June 1962	43	100	22·10 (159)	0·01	18 (S.)
<i>Argyresthia brockeella</i> (Hübner)	29	July 1963	35	100	23·48 (156)	0·00046	22 (N)
<i>ADELIDAE</i>							
<i>Adela fibulella</i> (Schiffermueller)	34	June 1962	20	36	21·10 (76)		34 (N)
				64	01·12 (45)	0·01	
<i>COLEOPTERA</i>							
<i>HYDROPHILIDAE</i>							
<i>Helophorus brevipalpis</i> Bedel	24	June 1962	119	44	10·28 (79)		34 (N)
				56	18·18 (90)	2100	
„ „ „	4	June, July 1962	29	41	10·50 (56)		34 (N)
				59	18·50 (78)	1500	
<i>Cercyon lugubris</i> (Olivier)	6	July 1962	7	100	13·26 (60)	8000	5 (N)
<i>Cercyon lateralis</i> (Marshall)	6	July 1962	90	18	06·12 (72)		29 (N)
				82	16·36 (136)	4100	
<i>Cercyon terminatus</i> (Marshall)	6	July 1962	282	18	11·48 (300)		40 (N)
				82	17·15 (45)	2700	
<i>Cercyon unipunctatus</i> (L.)	6	July 1962	20	15	03·24 (36)		29 (N)
				85	20·10 (80)	3·6	
<i>Cercyon quisquilius</i> (L.)	6	July 1962	85	25	11·42 (270)		40 (N)
				75	17·21 (69)	2700	
<i>Cercyon atricapillus</i> (Marshall)	6	July 1962	98	18	07·00 (36)		29 (N)
				82	16·00 (90)	4100	
<i>Megasternum obscurum</i> (Marshall)	14	Aug. 1962	32	66	10·01 (69)	7600	36 (N)
				34	16·19 (75)		
<i>Cryptopleurum minutum</i> (Fabr.)	6	July 1962	92	17	12·29 (220)		40 (N)
				83	17·45 (66)	2700	

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<i>COLEOPTERA (contd.)</i>							
SILPHIDAE							
<i>Catops</i> sp.	4	June 1962	11	100	16.24 (85)	500	9 (N)
" "	14 & 44	May 1962	27	100	12.50 (110)	8500	6 (N)
LEIODIDAE							
<i>Cyrtusa pauxilla</i> (Schmidt)	14	July 1962	40	100	18.36 (35)	1600	14 (N)
CLAMBIDAE							
<i>Clambus minutus</i> (Sturm)	44	May 1962	32	100	15.18 (84)	5000	9 (N)
<i>Clambus</i> sp.	45	May 1963	44	100	14.15 (87)	6700	9 (N)
SCYDMAENIDAE							
<i>Scydmaenus tarsatus</i> Mueller	6	July 1962	21	100	17.48 (36)	2700	10 (S.)
PTILIIDAE fig. 12							
<i>Acrotrichis</i> sp.	44	April 1962	77	100	14.36 (122)	5100	12 (N)
" "	21	July 1952	128	9	06.40 (90)		29 (N)
				91	16.58 (92)	4100	
Undetermined	3	April-July 1963	326	40	11.32 (183)		41 (N)
				60	15.42 (84)	4700	
"	3	April 1963	243	100	15.33 (82)	3800	9 (N)
"	2	Aug. 1959	160	20	13.30 (258)		40 (N)
				80	17.48 (72)	4500	
"	6	July 1962	1065	25	07.32 (78)		23 (N)
				75	15.48 (90)	4100	
STAPHYLINIDAE figs. 6, 16							
<i>Megarthus depressus</i> (Paykull)	6	July 1962	867	43	05.56 (55)		24 (S)
				57	17.06 (109)	2700	
<i>Megarthus denticollis</i> (Beck)	6	July 1962	68	48	05.48 (33)		23 (N)
				52	17.37 (58)	2700	
" " "	2	Aug. 1959 }	85	25	11.30 (68)		40 (N)
	43	Aug. 1960 }		75	17.56 (72)	6300	
<i>Proteinus ovalis</i> Stephens	44	April 1962	142	30	11.42 (80)		40 (N)
				70	17.56 (72)	5100	



## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D.) (in mins.) shown in brackets)	Light intensity (foot/ candles)	Curve type (shape shown in brackets)
<i>COLEOPTERA (contd.)</i>							
<i>STAPHYLINIDAE</i> figs. 6, 16 ( <i>contd.</i> )							
<i>Eusphalerum pallidum</i> (Gravenhorst)	28	July 1962	37	60	11·30 (242)	7000	40 (N)
				40	17·58 (24)		
<i>Trogophloeus</i> sp. [ <i>Carpelimus</i> sp.]	6	July 1962	645	17	07·52 (34)		37 (N)
				83	14·11 (104)	7000	
<i>Oxytelus sculptus</i> Gravenhorst	6	July 1962	42	100	18·09 (31)	1600	9 (N)
<i>Oxytelus complanatus</i> Erichson	6	July 1962	246	100	14·12 (178)	7000	12 (N)
<i>Oxytelus tetracarinatus</i> (Block)	6	July 1962	261	100	16·27 (30)	4100	10 (S.)
„ „ „	6	July 1962	225	85	16·55 (92)	8000	40 (N)
				15	10·30 (300)		
<i>Oxytelus tetracarinatus</i> (Block)	21	July 1952	120	100	18·58 (65)	1600	16 (S)
<i>Oxytelus complanatus</i> Erichson							
<i>Leucoparyphus silphoides</i> (L.)	6	July 1962	35	100	16·19 (112)	4100	12 (N)
<i>Oligota</i> sp.	6	July 1962	39	100	14·02 (42)	7000	11 (S)
<i>Autalia rivularis</i> (Gravenhorst)	6	July 1962	1130	95	14·41 (102)	7000	37 (N)
				5	07·18 (39)		
<i>Atheta longicornis</i> (Gravenhorst)	6	July 1962	336	20	07·36 (98)		29 (N)
				80	16·50 (102)	4100	
<i>Atheta</i> sp.	6	July 1962	371	24	07·42 (113)		39 (S)
				76	16·42 (86)	4100	
„ „	6	July 1962	318	100	12·58 (203)	9000	6 (N)
mixed spp.	15	June 1960	996	20	11·27 (268)		40 (N)
				80	18·18 (97)	7800	
„ „	44	April 1962	175	100	12·18 (150)	7500	6 (N)
<i>CANTHARIDAE</i>							
<i>Rhagonycha fulva</i> (Scopoli)	32	July 1952	181	100	16·19 (159)	4100	12 (N)
<i>Malthinus flaveolus</i> (Paykull)	45	June, July 1963	63	100	13·05 (383)	8800	43 (not illust.)
<i>Malthodes minimus</i> (L.)	45	June, July 1963	135	31	12·38 (342)		40 (N)
				69	18·30 (110)	5200	

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
COLEOPTERA (contd.)							
ELATERIDAE							
mixed spp.	45	May, June 1963	44	100	14·29 (184)	7300	12 (N)
HELODIDAE							
<i>Cyphon coarctatus</i> Paykull	29	July, Aug. 1963	23	30	06·32 (106)		29 (N)
				70	16·40 (194)	2100	
<i>Cyphon paykulli</i> Guérin-Ménéville	4	June, July 1962	46	100	15·18 (248)	6400	13 (S)
DERMESTIDAE							
<i>Anthrenus fuscus</i> Olivier	28	July 1962	49	100	11·48 (120)	9000	6 (N)
BYTURIDAE							
<i>Byturus tomentosus</i> (Degeer)	4	June, July 1962	32	100	15·54 (118)	5000	12 (N)
	37	July, Aug. 1962					
" " "	29	July, Aug. 1963					
			56	100	15·12 (163)	5600	12 (N)
NITIDULIDAE							
<i>Brachypterus glaber</i> (Stephens)	24	June 1962	708	100	12·42 (150)	9500	6 (N)
<i>Brachypterus urticae</i> (Fabr.)							
<i>Meligethes</i> sp.							
<i>Meligethes</i> sp.	16	July 1960	347	100	12·44 (136)	9000	6 (N)
<i>Epurea</i> sp.	28	July 1962	22	100	18·30 (74)	1600	14 (N)
	37	July 1962					
undetermined	21	July 1952	97	100	13·00 (172)	8000	6 (N)
CUCUJIDAE							
<i>Monotoma picipes</i> Herbst	6	July 1962	441	100	13·45 (106)	8000	6 (N)
CRYPTOPHAGIDAE fig. 6							
<i>Cryptophagus pubescens</i> Sturm	16	July 1960	21	100	19·01 (46)	600	14 (N)
<i>Cryptophagus pilosus</i> Gyllenhal							
<i>Cryptophagus</i> sp.							
	10	Aug. 1963	14	100	16·38 (53)	3000	9 (N)
<i>Atomaria lewisi</i> Reitter	2	Aug. 1959	63	15	10·42 (114)		39 (S)
				85	18·50 (58)	750	
" " "	6	July 1962	257	100	17·18 (120)	2700	12 (N)
<i>Atomaria pusilla</i> (Paykull)	6	July 1962	17	17	17·54 (23)		29 (N)
				83	15·44 (113)	5600	
<i>Atomaria fuscata</i> Schoenherr	21	July 1952	70	100	19·12 (55)	600	14 (N)
<i>Atomaria pusilla</i> (Paykull)							
<i>Atomaria lewisi</i> Reitter							
<i>Atomaria ruficornis</i> Marsham	6	July 1962	653	94	15·00 (130)	5600	29 (N)
				6	06·18 (150)		

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<i>COLEOPTERA (contd.)</i>							
<i>CRYPTOPHAGIDAE</i> fig. 6 ( <i>contd.</i> )							
<i>Atomaria</i> sp.	16	July 1960	67	100	16.25 (43)	4100	11 (.S)
<i>LATHRIDIIDAE</i>							
<i>Lathridius nodifer</i> Westwood [ <i>Aridius nodifer</i> (Westwood)]	44	April 1962	53	70	12.50 (146)	6300	40 (N)
				30	15.38 (16)		
<i>Enicmus transversus</i> Olivier	16	July 1960	183	35	12.36 (154)		40 (N)
<i>Corticarina fuscata</i> (Gyllenhal)							
<i>Corticarina gibbosa</i> (Herbst)				65	16.42 (94)	5600	
<i>Corticarina gibbosa</i> (Herbst)	21	July 1952	154	100	19.40 (43)	600	16 (.S)
<i>Corticarina gibbosa</i> (Herbst)	2	Aug. 1959	64	100	16.15 (195)	3000	12 (N)
<i>Corticarina fuscata</i> (Gyllenhal)							
mixed spp.	6	July 1962	64	22	11.08 (100)		40 (N)
				78	15.08 (120)	5600	
" "	28	July 1962	41	100	14.10 (134)	7000	12 (N)
<i>ANTHICIDAE</i>							
<i>Anthicus floralis</i> (L.)	6	July 1962	92	100	13.30 (120)	8000	6 (N)
<i>MORDELLIDAE</i>							
<i>Anaspis maculata</i> Geoffroy in Fourcroy	40	June 1962	25	100	13.12 (236)	8900	6 (N)
<i>Anaspis maculata</i> Geoffroy in Fourcroy	28	July 1962	63	100	13.30 (198)	8000	6 (N)
* <i>Anaspis ruficollis</i> Fabr.	28	July 1962	45	100	14.00 (228)	7000	6 (N)
<i>SCARABAEIDAE</i>							
<i>Serica brunnea</i> (L.)	29	June 1963	8	100	21.00 (65)	0.8	16 (.S)
<i>CHRYSOMELIDAE</i> fig. 6							
<i>Phyllotreta consobrina</i> (Curtis)	19	Oct. 1961	271	100	12.12 (78)	8100	5 (N)
<i>CURCULIONIDAE</i> figs. 3, 12							
<i>Phyllobius maculicornis</i> Germar	45	May–July 1963	155	100	13.40 (280)	9000	6 (N)
<i>Phyllobius argentatus</i> (L.)	45	May–July 1963	101	100	14.24 (318)	8000	12 (N)
<i>Ceuthorynchus contractus</i> Marsham	44	April, May 1962	6	100	12.24 (116)	8200	6 (N)
<i>Rynchaenus alni</i> (L.)	44	April, May 1962	9	100	11.17 (76)	8000	5 (N)
" " "	45	May 1963	365	100	12.57 (150)	8500	6 (N)
" " "	40	June 1963	98	100	13.12 (192)	8900	6 (N)

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D.) shown in brackets	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<b>STREPSIPTERA</b>							
<b>ELENCHIDAE fig. 15</b>							
<i>Elenchus tenuicornis</i> (Kirby) ♂	2	Aug. 1959	15	100	10·54 (196)	7600	6 (N)
<b>HYMENOPTERA</b>							
<b>TENTHREDINIDAE fig. 6</b>							
<i>Athalia cordata</i> Lepeletier	11	June 1962	252	100	12·39 (198)	9500	6 (N)
<i>Amauronematus amplus</i> Konow ♂	45	May 1963	152	100	07·33 (82)	3400	3 (N)
<b>BRACONIDAE fig. 3</b>							
<i>Chelonus scabrator</i> (Fabr.)	29	July 1963	33	100	12·55 (107)	9000	6 (N)
<i>Apanteles circumscriptus</i> (Nees)	38	Oct., Nov. 1963	371	100	12·50 (114)	3400	6 (N)
<i>Blacus</i> sp. mainly ♂	21	July 1952	261	100	15·31 (190)	5600	13 (.S)
<i>Aspilota</i> sp. ♀	21	July 1952	178	15	05·09 (127)		30 (.S)
				85	18·27 (53)	1600	
<i>Rizarcha areolaris</i> (Nees)	15	June 1961	557	100	10·36 (198)	8900	7 (S.)
<i>Daenusa maculipes</i> Thomson							
[ <i>Rizarcha maculipes</i> (Thomson)]	16	July 1960	428	100	12·57 (220)	9000	6 (N)
mixed Braconidae							
undetermined	29	July 1963	32	100	11·03 (78)	9000	5 (N)
<b>APHIDIIDAE fig. 12</b>							
<i>Trioxys angelicae</i> (Haliday) mainly ♂	21	July 1952	665	100	14·06 (276)	7000	13 (.S)
<b>ICHNEUMONIDAE</b>							
<i>Ichneumon</i> sp. ♂	29	July, Aug. 1963	97	100	12·24 (102)	9000	6 (N)
<i>Glypta trochanterata</i> Bridgman ♀	29	July 1963	22	100	13·44 (159)	8000	6 (N)
<i>Diplazon tetragonus</i> (Zetterstedt)	11	June 1962	41	100	15·17 (144)	6600	12 (N)
<i>Promethes cognatus</i> (Holmgren)							
<i>Promethes pulchellus</i> (Holmgren)							
* <i>Phaeogenes elongatus</i> Thunberg ♂	29	July 1963	32	100	11·03 (78)	9000	6 (N)
<b>CYNIPIDAE figs. 6, 15</b>							
<i>Neuroterus quercusbaccarum</i> (L.) ♂	39	June 1962	893	93	03·50 (70)	13·0	38 (.S)
				7	13·30 (230)		
" " " ♂	3	April 1963	127	100	13·20 (191)	6300	6 (N)
" " " ♂	3	May, June 1963	132	100	03·15 (74)	1·2	2 (.S)
<i>Charips arcuatus</i> Kieffer	21	July 1952	249	100	14·41 (261)	7000	13 (.S)
<i>Phaenoglyphis salicis</i> Cameron							
<i>Kleidotoma filicornis</i> Cameron ♀							
mixed Cynipidae	2	Aug. 1959	71	100	14·06 (160)	6300	12 (N)
	43	Aug. 1960					

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<i>HYMENOPTERA (contd.)</i>							
PTEROMALIDAE							
* <i>Macroglenes ocubitus</i> Westwood	28	July 1962	102	100	11·12 (180)	9000	6 (N)
* <i>Macroglenes oculatus</i> Westwood ♂	28	July 1962	20	100	12·11 (139)	9000	6 (N)
<i>Trichomalus campestris</i> Walker ♂	28	July 1962	37	100	14·02 (163)	7000	12 (N)
EULOPHIDAE fig. 12							
<i>Eulophus tidius</i> Walker	28	July 1962	111	100	14·10 (132)	7000	12 (N)
* <i>Ceraninus menes</i> (Walker)	28	July 1962	672	100	13·14 (164)	8000	6 (N)
<i>Aphelinus tibialis</i> (Nees)	28	July 1962	20	100	12·02 (116)	9000	6 (N)
MYMARIDAE figs. 3, 12							
undetermined	2	Aug. 1959	87	32	10·59 (99)		40 (N)
				68	16·37 (109)	3000	
"	15	June 1960	1101	100	12·32 (137)	9500	6 (N)
"	16	July 1960	29	100	14·04 (135)	7000	12 (N)
mixed Chalcidoidea	16	July 1960	110	100	13·24 (156)	8000	6 (N)
" "	28	July 1962	312	100	13·16 (153)	8000	6 (N)
DIAPRIIDAE							
<i>Ashmeadopria</i> sp.	28	July 1962	358	100	14·02 (166)	7000	12 (N)
PLATYGASTRIDAE fig. 12							
<i>Leptacis</i> sp.	21	July 1952	192	100	16·41 (119)	4100	13 (S)
mixed Platygastriidae	16	July 1960	427	100	15·03 (128)	5600	13 (S)
" "	28	July 1962	1270	100	12·34 (142)	9000	6 (N)
VESPIDAE							
<i>Vespula vulgaris</i> (L.)	2 Aug. 1959	}	74	100	11·37 (155)	8500	6 (N)
	43 Aug. 1960						
	10 Aug. 1963						
<i>Vespula rufa</i> (L.)	29 July, Aug. 1963		100	50	09·05 (154)	4100	23 (N)
				50	16·05 (149)		
APIIDAE figs. 1, 3							
<i>Bombus terrestris</i> (L.)	29	Aug. 1963	25	100	12·56 (141)	8500	6 (N)
<i>Bombus lapidarius</i> (L.)	29	July, Aug. 1963	15	100	13·36 (114)	7800	6 (N)
" " "	29	Aug. 1963	11	100	13·48 (112)	7600	6 (N)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<b>HYMENOPTERA (contd.)</b>							
<b>APIDAE figs. 1, 3 (contd.)</b>							
<i>Bombus pratorum</i> (L.) ♂	27	June, July 1963	47	100	12·54 (195)	9000	6 (N)
"    "    "    ♀	27	June, July 1963	142	100	13·12 (229)	8800	6 (N)
<i>Bombus agrorum</i> (Fabr.)	27	June, July 1963	26	100	13·35 (229)	8400	6 (N)
"    "    "    ♂	29	Aug. 1963	184	100	12·13 (142)	8500	6 (N)
"    "    "    ♀	29	Aug. 1963	43	100	12·00 (139)	8500	6 (N)
<i>Apis mellifera</i> L.	37	Sept. 1962	210	100	12·39 (108)	8100	6 (N)
<b>DIPTERA</b>							
<b>NEMATOCERA</b>							
<b>TIPULIDAE fig. 13</b>							
<i>Tipula oleracea</i> L.	24	May, June 1962	9	100	21·14 (72)	0·07	14 (N)
<i>Tipula paludosa</i> Meigen	14	Aug. 1962	289	100	21·12 (75)	0·00058	15 (S.)
"    "    "    "	14	Sept. 1962	1157	100	21·16 (93)	0·00008	18 (S.)
<i>Tipula fascipennis</i> Meigen	12	July 1963	25	100	20·50 (42)	3·6	15 (S.)
"    "    "    "	24	July 1963	97	100	23·06 (143)	0·00046	22 (N)
<i>Tipula lunata</i> L.	4	July 1962	10	100	22·18 (86)	0·0033	14 (N)
<i>Tipula</i> sp.	12	July 1963	144	14	02·24 (40)		29 (N)
				86	21·47 (51)	0·048	
"    "	29	May 1963	63	22	00·39 (86)		31 (S.)
				78	20·58 (47)	0·4	
<i>Nephrotoma flavescens</i> (L.)	16	July, Aug. 1960	12	50	20·14 (30)	1·2	23 (N)
				50	05·00 (150)		
<i>Nephrotoma quadrifaria</i> (Meigen)	4	June, July 1962	76	78	20·36 (30)	25	29 (N)
				22	03·42 (116)		
"    "    "    "	24	July 1963	38	100	21·04 (60)	0·048	14 (N)
<i>Limonia nubeculosa</i> Meigen	4	June, July 1962	194	50	21·30 (47)		40 (N)
				50	01·10 (190)	0·0032	
"    "    "    "	44	May 1962	48	28	21·40 (58)		28 (N)
				62	03·03 (33)	0·4	

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
DIPTERA (contd.)							
NEMATOCERA (contd.)							
TIPULIDAE fig. 9 (contd.)							
<i>Limonia nubeculosa</i> Meigen	37	Sept., Oct. 1962	413	46	18.46 (44)		41 (N)
				54	01.44 (232)	0.013	
" " "	11	June 1962	204	83	21.54 (43)	0.13	29 (N)
				17	02.12 (69)		
<i>Erioptera lutea</i> Meigen	24	May, June 1962	20	100	18.55 (60)	1100	14 (N)
<i>Ormosia nodulosa</i> (Macquart) ♂+♀	24	May, June 1962	186	50	14.04 (136)	5000	40 (N)
				50	17.51 (87)		
" " " ♂	24	May, June 1962	148	50	13.24 (144)	5800	40 (N)
				50	17.30 (90)		
" " " ♀	24	May, June 1962	38	100	17.18 (92)	3000	19 (S)
<i>Cheilotrichia cinerascens</i> (Meigen)	24	May, June 1962	36	100	19.38 (69)	360	14 (N)
undetermined	3	June, July 1963	51	25	03.07 (172)		29 (N)
				75	19.31 (115)	1.3	
"	3	June, July 1963	391	100	21.36 (57)	4.0	15 (S.)
"	3	June, July 1963	79	100	22.02 (120)	0.019	18 (S.)
TRICHO CERIDAE							
<i>Trichocera annulata</i> Meigen	33	Oct., Nov. 1962	582	85	16.24 (112)	35	29 (N)
				15	05.30 (176)		
" " "	42	March 1961	143	100	17.57 (46)	600	14 (N)
" " "	6	Oct. 1962	674	70	17.52 (148)	0.95	37 (N)
				30	08.14 (84)		
<i>Trichocera regelationis</i> (L.)	44	Mar., April 1962	286	100	17.24 (122)	950	17 (N)
" " "	19	Sept., Oct. 1961	137	58	19.24 (104)	0.06	25 (S.)
				42	05.18 (153)		
ANISOPIDAE fig. 10							
<i>Anisopus fenestralis</i> (Scopoli)	15	June 1960	11	73	20.27 (28)	13	29 (N)
				27	03.57 (24)		

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<b>DIPTERA (cont.)</b>							
<b>NEMATOCERA (contd.)</b>							
<b>ANISOPIDAE fig. 10 (contd.)</b>							
<i>Anisopus fenestralis</i> (Scopoli)	5	April 1956	2737	100	15·24 (198)	3800	12 (N)
„ „ „	5	May 1956	13,790	40	10·52 (206)		35 (.S)
				60	20·37 (56)	0·4	
„ „ „	5	June 1956	13,267	70	12·40 (449)		42 (N)
				30	21·25 (43)	0·13	
„ „ „	5	July 1956	14,395	47	07·48 (300)		35 (.S)
				53	21·00 (65)	0·048	
„ „ „	5	Aug. 1956	15,152	50	10·42 (254)		35 (.S)
				50	19·46 (103)	8·0	
„ „ „	5	Sept. 1956	25,441	50	14·12 (287)		35 (.S)
				50	19·20 (46)	0·0048	
„ „ „	5	Oct. 1956	3974	100	14·15 (200)	2500	13 (.S)
„ „ „	5	Nov. 1956	1098	100	13·55 (120)	1900	13 (.S)
„ „ „	5	Dec. 1956	1383	100	12·45 (187)	1800	8 (.S)
„ „ „	5	Jan. 1957	176	40	08·27 (69)	800	24 (.S)
				60	15·30 (69)		
„ „ „	5	Feb. 1957	235	100	16·04 (191)	740	13 (.S)
„ „ „	5	March 1957	9154	37	08·42 (136)		30 (.S)
				63	16·41 (65)	1550	
„ „ „	5	April 1957	3887	60	12·30 (120)	7500	35 (.S)
				40	18·48 (140)		
„ „ „	5	May 1957	5550	50	11·15 (225)		35 (.S)
				50	20·04 (69)	0·4	
„ „ „	5	June 1957	8245	46	09·30 (134)		35 (.S)
				54	20·39 (103)	13	



## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D.) (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
DIPTERA (contd).							
NEMATOCERA (contd.)							
ANISOPIDAE fig. 10 (contd.)							
<i>Anisopus fenestralis</i> (Scopoli)	5	July 1957	4513	30	06·28 (171)		39 (S)
				70	20·34 (78)	3·6	
" " "	5	Aug. 1957	1391	29	07·51 (230)		39 (S)
				71	20·00 (86)	0·023	
" " "	5	Sept. 1957	1848	22	07·06 (159)		30 (S)
				78	18·09 (104)	2·8	
" " "	5	Oct. 1957	4835	17	06·00 (133)		39 (S)
				83	16·18 (65)	570	
PTYCHOPTERIDAE fig. 13							
<i>Ptychoptera contaminata</i> (L.)	4	June, July 1962	83	100	13·44 (136)	8300	6 (N)
<i>Ptychoptera albimana</i> (Fabr.)	44	May 1962	12	100	12·18 (115)	8500	6 (N)
" " "	3	May 1963	30	100	12·26 (160)	8500	6 (N)
PSYCHODIDAE figs. 10, 13							
<i>Pericoma nubila</i> (Meigen)	4	June, July 1962	803	28	08·30 (103)		30 (S)
				72	16·07 (79)	6200	
" " "	24	Oct. 1962	122	100	12·34 (92)	4800	13 (S)
<i>Pericoma fusca</i> (Macquart)	4	June, July 1962	299	58	16·03 (121)	7000	30 (S)
				42	09·08 (152)		
<i>Pericoma</i> sp.	3	May 1963	1007	100	11·32 (176)	8500	7 (S)
<i>Clytocerus ocellaris</i> (Meigen)	24	May, June 1962	141	100	13·54 (151)	8000	13 (S)
<i>Telmatoscopus ustulatus</i> (Walker)	2	Aug. 1959	246	100	20·00 (101)	0·023	17 (N)
<i>Psychoda alternata</i> Say	24	May 1962	661	100	18·33 (126)	1100	17 (N)
<i>Psychoda phalaenoides</i> (L.)	44	April 1962	458	60	17·16 (157)	1500	41 (N)
" " "				40	02·30 (337)		
<i>Psychoda albipennis</i> Zetterstedt	42	March 1961	657	88	17·30 (120)	600	29 (N)
				12	05·56 (112)		

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
DIPTERA (contd.)							
NEMATOCERA (contd.)							
PSYCHODIDAE figs. 10, 13 (contd.)							
<i>Psychoda brevicornis</i> Tonnoir	15	June 1960	789	33	03·53 (185)		29 (N)
				67	19·42 (98)	950	
<i>Psychoda</i> sp.	43	Aug. 1960	1862	85	19·58 (105)	8·0	29 (N)
				15	04·36 (131)		
CULICIDAE figs. 5, 13							
<i>Chaoborus crystallinus</i> (Degeer) ♂	44	April, May 1962	297	100	12·36 (131)	8000	6 (N)
<i>Culex pipiens</i> L. ♂ + ♀	15	June 1960	66	73	21·00 (32)	0·13	31 (S.)
				27	02·45 (42)		
„ „ „ ♂	16	June, July 1960	66	90	20·56 (24)	0·6	31 (S.)
				10	03·04 (20)		
„ „ „ ♀	4	July 1962	274	95	20·30 (56)	3·6	31 (S.)
				5	03·52 (70)		
„ „ „ ♀	24	July 1963	1062	61	21·06 (82)	0·048	31 (S.)
				39	01·32 (124)		
„ „ „ ♀	24	July 1963	277	87	20·56 (41)	3·6	31 (S.)
				13	03·10 (20)		
„ „ „ ♂	24	July 1963	506	72	21·12 (91)	0·048	31 (S.)
				28	03·06 (133)		
„ „ „ ♂ + ♀	24	July 1963	1845	70	21·04 (70)	0·048	31 (S.)
				30	01·57 (127)		
undetermined	3	June, July 1963	33	94	21·30 (80)	0·2	29 (N)
				6	02·45 (18)		
CHIRONOMIDAE figs. 13, 16							
<i>Pentaneura monilis</i> (L.) ♀	3	April 1963	55	38	04·23 (195)		29 (N)
				62	18·53 (74)	520	
„ „ „ ♂	3	April 1963	50	30	04·26 (321)		29 (N)
				70	19·40 (50)	1·5	

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
DIPTERA (contd.)							
NEMATOCERA (contd.)							
CHIRONOMIDAE figs. 13, 16 (contd.)							
<i>Pentaneura nubila</i> (Meigen)	4	July 1962	209	100	20.20 (27)	3.6	14 (N)
<i>Hydrobaenus semivirens</i> (Kieffer)	15	Aug. 1960	591	70	09.36 (66)	6300	28 (N)
				30	15.28 (150)		
<i>Hydrobaenus foliaceus</i> (Kieffer)	44	March 1962	795	100	13.18 (96)	5500	8 (.S)
"      "      "      ♂+♀	42	March 1961	122	100	15.03 (294)	2800	19 (.S)
"      "      "      ♂+♀	2	Aug. 1959	302	88	10.00 (32)	7600	36 (N)
				12	17.02 (130)		
<i>Chironomus</i> sp. ♀	2	Aug. 1959	179	33	12.19 (152)		37 (N)
				67	19.37 (93)	5.0	
"      "      ♀	4	July 1962	54	100	20.38 (60)	3.6	14 (N)
<i>Tanytarsus brunnipes</i> Zetterstedt	25	Oct. 1962	550	50	07.10 (252)	0.95	23 (N)
				50	17.04 (127)		
<i>Tanytarsus subviridis</i> Goetghebuer	25	Oct. 1962	163	70	17.16 (60)	0.95	29 (N)
				30	07.46 (87)		
<i>Tanytarsus atrofasciatus</i> Kieffer ♂	25	Oct. 1962	65	100	17.08 (94)	0.95	19 (.S)
"      "      "      ♀	24	June 1962	105	100	19.38 (58)	950	14 (N)
<i>Tanytarsus tenuis</i> (Meigen)	25	Oct. 1962	270	83	17.06 (53)	0.95	37 (N)
				17	09.12 (52)		
<i>Tanytarsus photophilus</i> Goetghebuer ♀	25	Oct. 1962	132	100	17.06 (39)	0.95	14 (N)
<i>Tanytarsus manicus</i> (Walker)							
CERATOPOGONIDAE fig. 16							
<i>Forcipomyia bipunctata</i> (L.)	21	July 1952	505	95	19.04 (114)	600	30 (.S)
				5	03.40 (103)		
<i>Culicoides obsoletus</i> (Meigen)	39	May, June 1962	69	100	19.52 (36)	104	14 (N)
"      "      "	2	Aug. 1959	120	100	18.36 (155)	750	17 (N)
"      "      "	43	Aug. 1960					
* <i>Culicoides impunctatus</i> Goetghebuer	8	Aug. 1958	18,950	Flight throughout 24 hours		0.00058	43 (not illust.)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
DIPTERA (contd.)							
NEMATOCERA (contd.)							
BIBIONIDAE fig. 6							
<i>Dilophus febrilis</i> (L.) ♂	24	May, June 1962	64	100	13·18 (120)	8500	7 (S.)
"    "    " ♂	14	June 1962	610	100	11·30 (80)	9500	5 (N)
SCATOPSIDAE							
<i>Psectrosciaria tenuicauda</i> Duda	28	July 1962	1218	100	11·30 (103)	9000	7 (S.)
<i>Swammerdamella brevicornis</i> (Meigen)	28	July 1962	135	100	11·16 (146)	9000	7 (S.)
"    "    "	15	July 1961	409	100	12·52 (118)	9000	7 (S.)
mixed spp.	2 43	Aug. 1959 } Aug. 1960 }	21	100	12·24 (147)	8500	7 (S.)
MYCETOPHILIDAE figs. 10, 13							
<i>Allodia</i> sp.	25	Oct. 1962	91	67	16·10 (48)	570	29 (N)
				33	09·54 (177)		
<i>Mycetophila fungorum</i> (Degeer)	46	Sept. 1960	1792	50	05·30 (70)	2·8	23 (N)
				50	18·42 (117)		
"    "    "	25	Oct. 1962	42	100	18·34 (92)	0·002	18 (S.)
"    "    "	44	May 1962	77	100	20·08 (50)	0·4	15 (S.)
<i>Mycetophila ocellus</i> Walker	44	May 1962	245	100	17·42 (84)	2150	14 (N)
"    "    "	4	July 1962	76	90	19·36 (56)	600	29 (N)
				10	05·18 (38)		
"    "    "	25	Oct. 1962	55	87	16·36 (56)	570	29 (N)
				13	07·48 (32)		
Mycetophilinae (mixed spp.)	4	July 1962	198	100	19·26 (84)	600	16 (S)
"    "    "	25	Oct. 1962	87	100	12·28 (196)	4800	6 (N)
Sciarinae (undetermined)	42	March 1961	34	100	13·40 (108)	5500	5 (N)
"    "	32	July 1957	862	65	18·20 (150)	1600	40 (N)
				35	11·50 (210)		
"    "	6	Oct. 1962	361	100	13·36 (117)	3700	6 (N)
"    "	44	Mar., April 1962	938	100	13·30 (167)	5700	6 (N)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D.) (in mins.) shown in brackets	Light intensity (foot/ candles)	Curve type (shape shown in brackets)
<b>DIPTERA (contd.)</b>							
<b>NEMATOCERA (contd.)</b>							
CECIDOMYIIDAE figs. 6, 13							
<i>Lestremia</i> sp.	42	March 1961	87	100	13·10 (122)	5500	6 (N)
Lestremiinae (undetermined)	44	Mar., April 1962	186	100	13·14 (140)	6000	6 (N)
„ „	16	July 1960	184	100	10·40 (83)	8000	5 (N)
„ „	15	June 1960	1028	100	10·10 (140)	8900	6 (N)
Cecidomyiinae (undetermined)	2	Aug. 1959	2547	100	19·52 (53)	8·0	15 (S.)
„ „	43	Aug. 1960	1920	100	20·08 (84)	0·023	15 (S.)
„ „	28	July 1962	645	100	21·24 (100)	0·048	15 (S.)
„ „	21	July 1952	4086	100	22·54 (96)	0·0033	21 (S.)
<i>Xylopriona</i> sp.	15	June 1960	2677	100	22·22 (188)	0·01	21 (S.)
„ „	16	July 1960	1020	100	20·54 (94)	3·6	15 (S.)
<b>BRACHYCERA</b>							
STRATIOMYIDAE							
<i>Beris chalybeata</i> (Forster)	11	June 1962	23	100	13·54 (127)	8900	6 (N)
<i>Microchrysa polita</i> (L.)	6	July 1962	17	100	12·42 (214)	9000	6 (N)
RHAGIONIDAE							
<i>Rhagio lineola</i> Fabr.	29	July, Aug. 1963	46	100	14·07 (343)	7200	13 (S)
TABANIDAE							
<i>Haemotopota pluvialis</i> (L.)	8	June–Sept. 1957	41	100	15·27 (170)	5200	13 (S)
EMPIDIDAE fig. 3							
<i>Tachydromia arrogans</i> (L.)	3, 11, 14	June 1962	43	100	15·36 (201)	6600	12 (N)
<i>Platypalpus minutus</i> (Meigen)	24	May, June 1962	10	100	12·45 (153)	9000	6 (N)
<i>Platypalpus pallidiventris</i> (Meigen)	21	July 1952	207	50	12·48 (228)		41 (N)
				50	18·14 (104)	5600	
<i>Hilara</i> sp.	24	May, June 1962	144	80	18·08 (56)	2700	37 (N)
				20	11·18 (112)		
„ „	3	June, July 1963	53	100	12·52 (228)	9000	6 (N)
„ „	3	June, July 1963	181	100	14·43 (206)	7200	12 (N)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
<b>DIPTERA (contd.)</b>							
<b>BRACHYCERA (contd.)</b>							
<b>EMPIDIDAE fig. 3 (contd.)</b>							
<i>Empis livida</i> L.	27	June, July 1963	30	50	08·48 (125)		23 (N)
				50	17·45 (88)	2700	
<i>Empis nuntia</i> Meigen	29	May 1963	62	21	07·54 (120)		37 (N)
				79	17·35 (28)	5000	
<i>Empis aestiva</i> Loew	24	May, June 1962	24	68	11·18 (92)	9000	36 (N)
				32	18·38 (80)		
<i>Rhamphomyia</i> sp.	28	July 1962	508	100	12·30 (127)	9000	6 (N)
<i>Phyllodromia melanocephala</i> (Fabr.)	29	July, Aug. 1963	237	100	14·02 (231)	8600	13 (S)
undetermined	3	June, July 1963	22	100	13·05 (128)	8900	6 (N)
"	6	Oct. 1962	20	100	14·06 (150)	2500	13 (S)
"	24	May, June 1962	46	100	14·20 (207)	7400	12 (N)
<b>DOLICHOPODIDAE fig. 3</b>							
<i>Dolichopus unguatus</i> (L.)	11	June 1962	73	68	07·26 (60)	5000	36 (N)
				32	13·12 (60)		
" " "	4	June, July 1962	1093	100	13·20 (132)	8600	6 (N)
<i>Xiphandrium caliginosum</i> (Meigen) }	24	May, June 1962	40	100	13·10 (172)	8400	6 (N)
<i>Syntormon pallipes</i> (Fabr.) }							
<i>Chrysotus gramineus</i> (Fallén)	21	July 1952	341	50	08·00 (104)		24 (S)
				50	17·21 (68)	2700	
<i>Sciopus platypterus</i> (Fabr.)	4	June, July 1962	77	67	17·44 (66)	5800	24 (S)
				33	07·42 (96)		
undetermined	4	June, July 1962	370	100	13·30 (146)	8500	6 (N)
"	15	July 1961	218	100	14·16 (184)	7000	12 (N)
<b>PHORIDAE</b>							
<i>Megaselia halterata</i> (Wood) ♂ + ♀	7	Aug. 1963	35,960	50	10·43 (108)	7600	41 (N)
				50	15·03 (153)		
" " " ♂	7	Sept. 1963	35,058	60	10·48 (110)	6900	41 (N)
				40	15·06 (148)		

## APPENDIX B.—continued

APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
DIPTERA (contd.)							
BRACHYCERA (contd.)							
PHORIDAE (contd.)							
<i>Megaselia halterata</i> (Wood) ♀	7	Sept. 1963	4375	50	10·51 (89)	6900	41 (N)
				50	14·50 (151)		
<i>Megaselia</i> sp.	34	June 1962	1170	100	12·39 (240)	9500	6 (N)
<i>Megaselia</i> spp.	19	Oct. 1961	180	100	13·33 (153)	3700	6 (N)
“ ”	21	July 1952	163	30	09·48 (91)		37 (N)
				70	17·04 (90)	2700	
undetermined	2	Aug. 1959	90	100	14·28 (216)	6300	12 (N)
	43	Aug. 1960					
CYCLORRHAPHA							
DORILAIIDAE							
<i>Dorilas</i> sp.	29	July, Aug. 1963	41	100	13·22 (160)	8000	6 (N)
“ ”	29	July, Aug. 1963	32	100	13·50 (120)	7500	6 (N)
SYRPHIDAE fig. 17							
<i>Helophilus pendulus</i> (L.) ♂ + ♀	29	July, Aug. 1963	28	100	12·28 (119)	8800	6 (N)
<i>Zelima segnis</i> (L.) ♂ + ♀	29	Aug. 1963	29	100	13·03 (101)	7600	6 (N)
<i>Syrpitta pipiens</i> (L.)	29	July, Aug. 1963	33	100	09·50 (93)	7200	4 (N)
<i>Rhingia macrocephala</i> (Harris)	29	Aug. 1963	86	100	12·15 (114)	8500	6 (N)
<i>Neoascia podagrica</i> (Fabr.)	24	May, June 1962	87	100	12·42 (133)	9000	6 (N)
<i>Neoascia</i> spp.	29	Aug. 1963	774	100	12·41 (109)	8500	6 (N)
<i>Melanostoma mellinum</i> (L.) ♂ + ♀	29	July, Aug. 1963	47	100	11·06 (238)	8400	6 (N)
<i>Melanostoma scalare</i> (Fabr.) ♂ + ♀	29	Aug. 1963	172	100	12·26 (146)	8500	6 (N)
<i>Platycheirus timeo</i> (Harris) ♂	29	Aug. 1963	105	100	11·45 (94)	8500	6 (N)
<i>Episyrphus balteatus</i> (Degeer) ♀	29	Aug. 1963	184	100	12·20 (92)	8500	6 (N)
“ ” “ ♂	29	Aug. 1963	323	100	12·21 (97)	8500	6 (N)
<i>Scaeva pyrastris</i> (L.)	29	Aug. 1963	12	100	13·05 (92)	7600	8 (N)
<i>Metasyrphus consisto</i> Harris ♂	45	June 1963	190	100	09·10 (92)	7800	4 (N)
<i>Syrphidis ribesii</i> (L.) ♀	29	Aug. 1963	651	100	12·42 (114)	8500	6 (N)
“ ” “ ♂	29	Aug. 1963	569	100	12·51 (105)	8500	6 (N)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/candles)	Curve type (shape shown in brackets)
DIPTERA (contd.)							
CYCLORRHAPHA (contd.)							
SYRPHIDAE fig. 17 (contd.)							
<i>Syrphidis vitripennis</i> (Meigen) ♂	29	Aug. 1963	39	100	12.28 (112)	8500	6 (N)
"      "      "      ♀	29	Aug. 1963	25	100	12.19 (80)	8500	5 (N)
PALLOPTERIDAE							
<i>Palloptera ustulata</i> Fallén	24	July 1963	9	100	17.54 (115)	2700	12 (N)
<i>Palloptera umbellatarum</i> (Fabr.)	4	June, July 1962	26	100	17.18 (97)	3300	12 (N)
"      "      "	24	July 1963	4	100	17.38 (23)	2700	9 (N)
TRYPETIDAE							
<i>Urophora jaceana</i> (Hering)	12	July 1963	13	100	12.33 (115)	9000	6 (N)
<i>Trypeta cylindrica</i> (Robineau-Desvoidy)	29	July, Aug. 1963	22	100	12.26 (154)	8800	6 (N)
LONCHAEIDAE							
<i>Lonchaea flavidipennis</i> Zetterstedt	10	Aug. 1963	18	100	11.54 (279)	8500	6 (N)
LAUXANIIDAE							
<i>Cnemocantha rorida</i> (Fallén)	11	June 1962	18	60	18.30 (199)	2100	34 (N)
				40	03.20 (140)		
<i>Cnemocantha</i> spp.	29	July, Aug. 1963	12	100	17.12 (146)	2500	12 (N)
	12	July 1963					
SEPSIDAE							
<i>Sepsis fulgens</i> Meigen	21	July 1952	2594	100	14.16 (140)	7000	12 (N)
"      "      "	6	July 1962	431	100	14.08 (214)	7000	12 (N)
HELOMYZIDAE							
<i>Tephrochlamys rufiventris</i> (Meigen)	6	Oct. 1962	12	100	15.56 (18)	1400	16 (.S)
OPOMYZIDAE							
<i>Opomyza germinationis</i> (L.)	29	July, Aug. 1963	11	100	16.06 (105)	4100	12 (N)
<i>Opomyza germinationis</i> (L.)	14	Sept., Oct. 1962	160	40	08.19 (177)		23 (N)
<i>Geomyza tripunctata</i> Fallén			60	15.30 (156)	2100		
EPHYDRIDAE							
<i>Hydropota</i> sp.	24	May, June 1962	85	100	14.02 (130)	7800	12 (N)
SPHAEROCERIDAE							
<i>Sphaerocera curvipes</i> Latreille	6	Oct. 1962	347	100	12.24 (99)	4800	6 (N)



## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/ candles)	Curve type (shape shown in brackets)
<b>DIPTERA (contd.)</b>							
<b>CYCLORRHAPHA (contd.)</b>							
<b>SPHAEROCERIDAE (contd.)</b>							
<i>Trichiaspis similis</i> (Collin)	6	Oct. 1962	806	74	12.04 (174)	2500	42 (N)
				26	15.48 (96)		
<i>Limosina clunipes</i> (Meigen)	6	July 1962	652	100	13.50 (149)	8000	7 (S.)
<i>Limosina</i> sp.	6	July 1962	803	100	14.05 (116)	7000	12 (N)
<i>Coprophila acutangula</i> (Zetterstedt)	6	July 1962	44	100	14.00 (240)	7000	7 (S.)
<i>Coprophila ferruginata</i> (Stenhammer)	6	July 1962	122	100	09.17 (105)	7000	4 (N)
<i>Coprophila vagans</i> (Haliday)	24	May 1962	470	32	10.48 (111)		37 (N)
				68	18.34 (65)	1100	
undetermined	6	July 1962	4311	100	14.04 (157)	7000	12 (N)
<b>DROSOPHILIDAE figs. 1, 5, 10</b>							
<i>Drosophila disticha</i> (Duda) ♀ [ <i>Parascaptomyza pallida</i> (Zetterstedt)]	21	July 1952	152	91	20.24 (35)	3.6	29 (N)
				9	04.30 (104)		
„ „ „ ♂	21	July 1952	230	81	20.26 (52)	3.6	29 (N)
				19	05.10 (167)		
„ „ „	19	Oct. 1961	44	100	12.04 (268)	4800	6 (N)
„ „ „	6	Oct. 1962	49	100	14.48 (108)	2500	13 (S)
<i>Drosophila graminum</i> (Fallén) ♀ [ <i>Scaptomyza graminum</i> (Fallén)]	21	July 1952	33	79	20.28 (45)	3.6	29 (N)
				21	03.58 (43)		
„ „ „ ♂	21	July 1952	76	87	20.39 (36)	3.6	29 (N)
				13	04.20 (39)		
<i>Drosophila Subobscura</i> (Collin) ♀	21	July 1952	150	57	20.20 (46)	3.6	23 (N)
				43	04.15 (40)		
„ „ „ ♂	21	July 1952	1049	32	20.15 (64)		33 (S)
				68	03.59 (38)	3.6	
„ „ „ ♂ + ♀	37	Oct. 1953	20	30	17.10 (38)		33 (S)
				70	07.30 (35)	3.0	
<i>Drosophila busckii</i> Coquillett	6	Oct. 1962	25	100	15.34 (50)	1400	16 (S)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D. (in mins.) shown in brackets)	Light intensity (foot/ candles)	Curve type (shape shown in brackets)
DIPTERA (contd.)							
CYCLORRHAPHA (contd.)							
DROSOPHILIDAE figs. 1, 5, 10 (contd.)							
<i>Drosophila</i> spp.	21	July 1952	1767	50	03·52 (26)	3·6	24 (.S)
				50	20·10 (27)		
AGROMYZIDAE							
<i>Ceradontha spinicornis</i> (Macquart)	14	Aug., Sept. 1962	48	100	13·54 (170)	6800	6 (N)
<i>Phytomyza</i> sp.	32	July 1957	302	64	11·24 (274)	8000	42 (N)
				36	17·12 (96)		
CHLOROPIDAE figs. 1, 3, 10, 12							
<i>Oscinella frit</i> (L.) ♀	15	June 1960	2348	100	13·42 (179)	8900	6 (N)
„ „ „ ♂	15	June 1960	2957	100	13·51 (173)	8900	8 (.S)
„ „ „ ♀	14	June 1962	522	100	13·34 (166)	8900	6 (N)
„ „ „ ♂	14	June 1962	763	100	13·18 (134)	8900	6 (N)
<i>Thaumatomyia notata</i> (Meigen)	21	July 1952	242	40	08·35 (104)		24 (.S)
				60	17·42 (79)	2700	
„ „ „	19	Oct. 1961	153	100	13·30 (120)	3700	8 (.S)
CORDILURIDAE							
<i>Scopeuma stercorarium</i> (L.) ♀	6	Oct. 1962	724	100	13·09 (123)	3700	6 (N)
„ „ „ ♂	6	Oct. 1962	556	100	13·20 (129)	3700	6 (N)
CALLIPHORIDAE							
<i>Calliphora erythrocephala</i> (Meigen)	37	Sept., Oct. 1962	51	100	12·30 (92)	6400	6 (N)
<i>Lucilia caesar</i> (L.)	37	Sept., Oct. 1962	451	100	13·04 (120)	5800	6 (N)
„ „ „	29	Aug. 1963	243	100	11·52 (94)	8500	6 (N)
<i>Lucilia</i> sp.	29	Aug. 1963	55	100	11·48 (156)	8500	6 (N)
MUSCIDAE figs. 1, 3							
<i>Musca autumnalis</i> Degeer	12	July 1963	51	100	08·43 (112)	5600	4 (N)
<i>Phaonia variegata</i> (Meigen)	37	Sept., Oct. 1962	293	100	11·30 (170)	6300	6 (N)
<i>Phaonia rufipalpis</i> (Macquart)	4	June, July 1962	245	100	13·38 (200)	8400	6 (N)
* <i>Phaonia humerella</i> Stein	37	Sept., Oct. 1962	227	100	12·42 (139)	6000	6 (N)

## APPENDIX B.—continued

Species	Site No.	Month & year	Total catch	Percentage population represented	Mean flight time(s) G.M.T. (S.D.) (in mins.) shown in brackets)	Light intensity (foot/ candles)	Curve type (shape shown in brackets)
<b>DIPTERA (contd.)</b>							
<b>CYCLORRHAPHA (contd.)</b>							
<b>MUSCIDAE figs. 1, 3 (contd.)</b>							
<i>Hylemya</i> sp. <i>sensu strictu</i>	39	May, June 1962	171	100	13·06 (94)	8600	6 (N)
"    "    "    "	44	May 1962	112	100	13·30 (96)	7800	6 (N)
<i>Pegohylemyia</i> sp.	2	Aug. 1959 }	188	100	13·56 (140)	7600	6 (N)
	43	Aug. 1960 }					
"    "	15	July 1960	136	100	12·12 (210)	9000	6 (N)
<i>Coenosia tricolor</i> (Zetterstedt)	24	June 1962	31	100	13·12 (181)	8900	6 (N)
<i>Coenosia sexnotata</i> Meigen	4	June, July 1962	336	100	12·38 (206)	9200	6 (N)

(Figure 18 see overleaf)

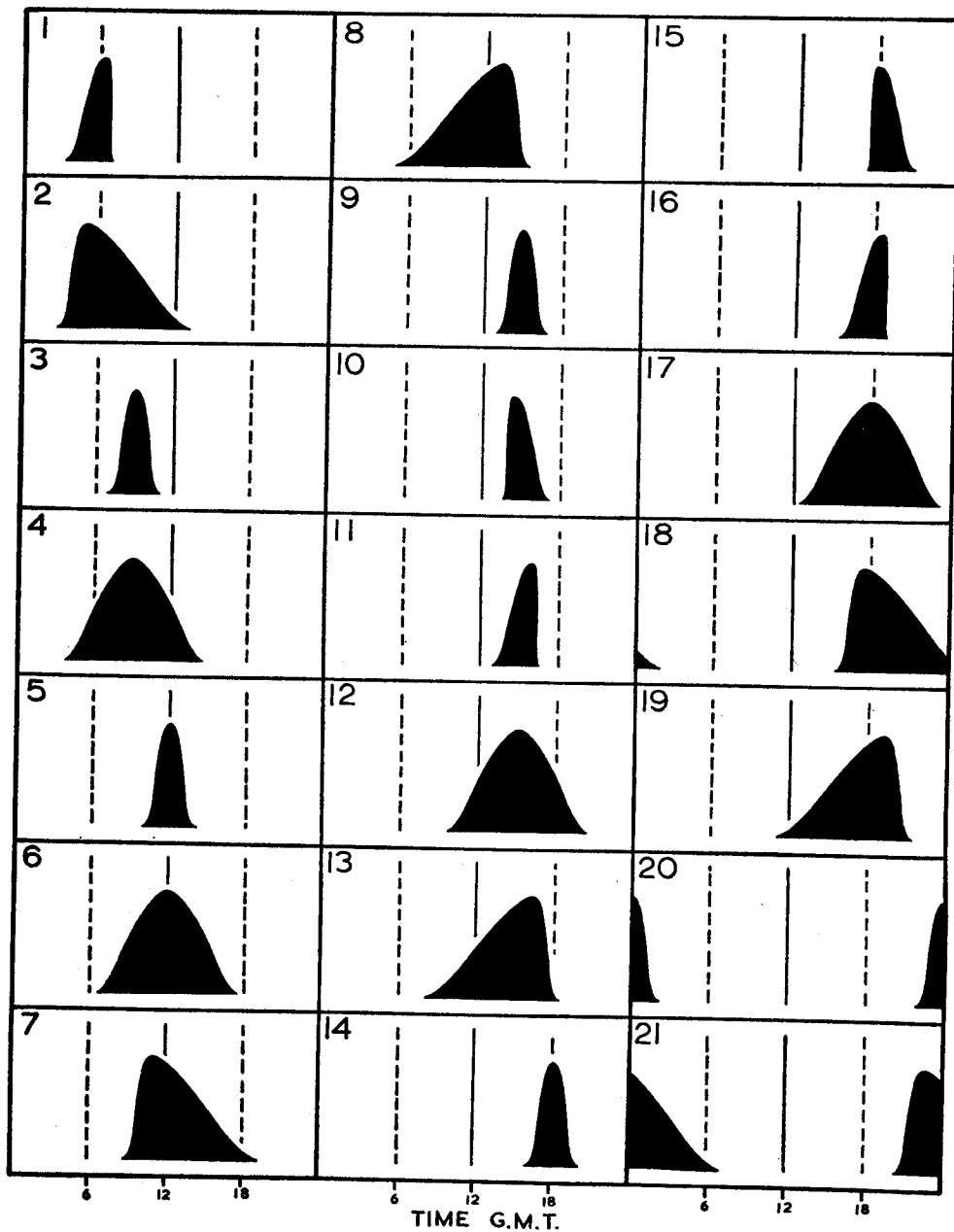


FIG. 18.—Classification of the 42 types of flight distribution curve recorded. Each insect taxon in *Appendix B* is referred to one of these curves by number. See also p. 398

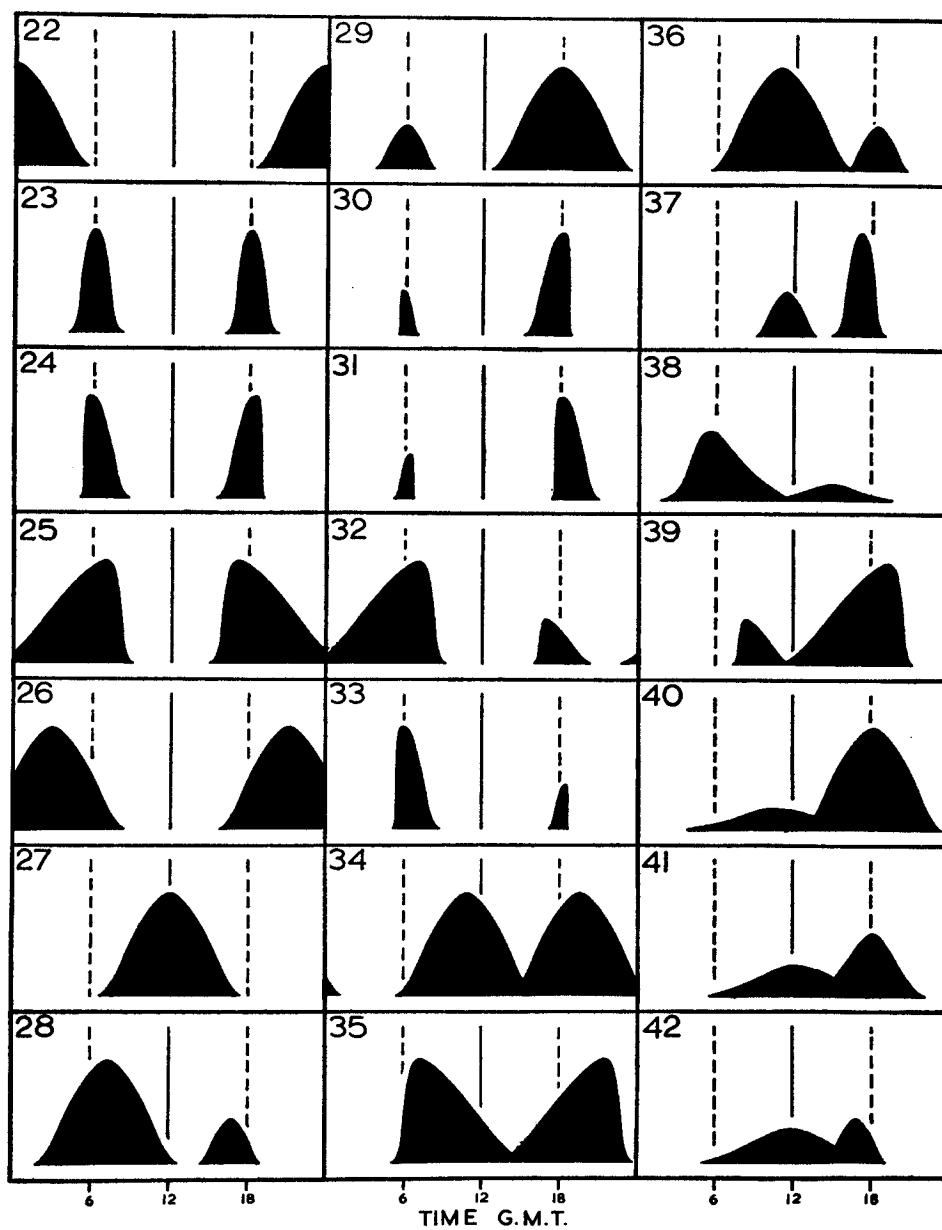


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