

Diurnal periodicity of flight by insects

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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, 1950*a*; 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.

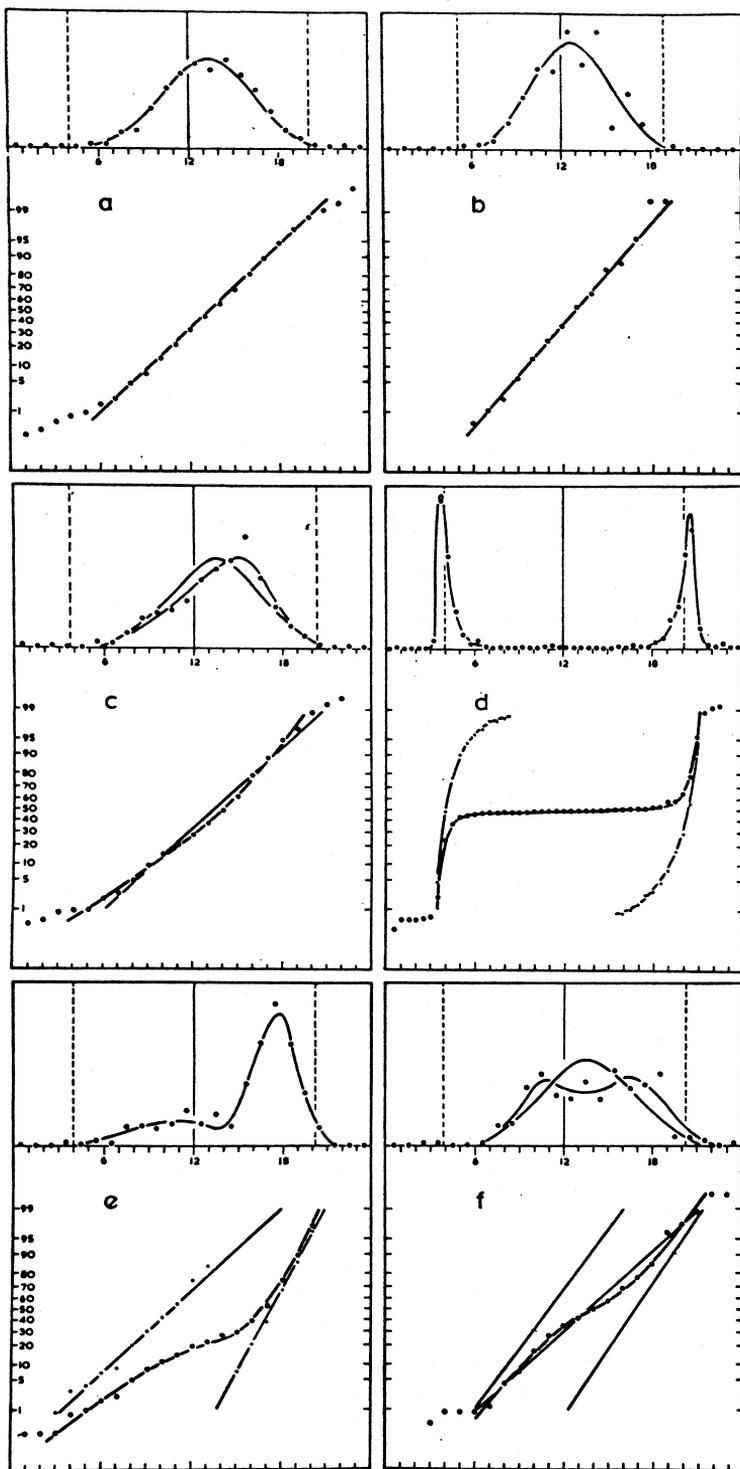


FIG. 1.—Fitting probability curves to flight periodicity samples. (a) *Oscinella frit* (Chloropidae), females, July 1960; (b) *Bombus agrorum* (Apidae), August 1963; (c) *Oscinella frit*, males, June 1960; (d) Drosophilidae, July 1952; (e) *Cavariella aegopodii* (Aphididae), July 1949; (f) *Phaonia rufipalpis* (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

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.

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.

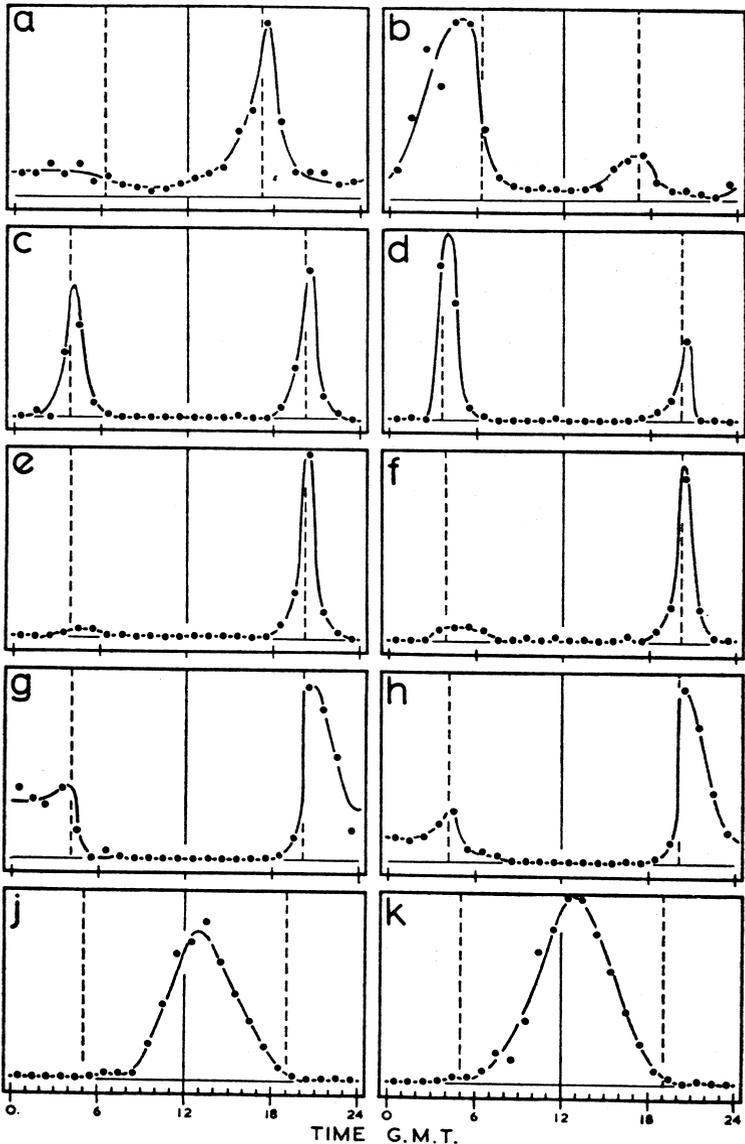


FIG. 5.—Periodicity curves for different sexes. *Lithocolletis messaniella* (Gracillariidae: Lep.): (a) females; (b) males. *Drosophila subobscura* (Drosophilidae: Dipt.): (c) females; (d) males. *Drosophila disticha* (Drosophilidae: Dipt.): (e) females; (f) males. *Culex pipiens* (Culicidae: Dipt.):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

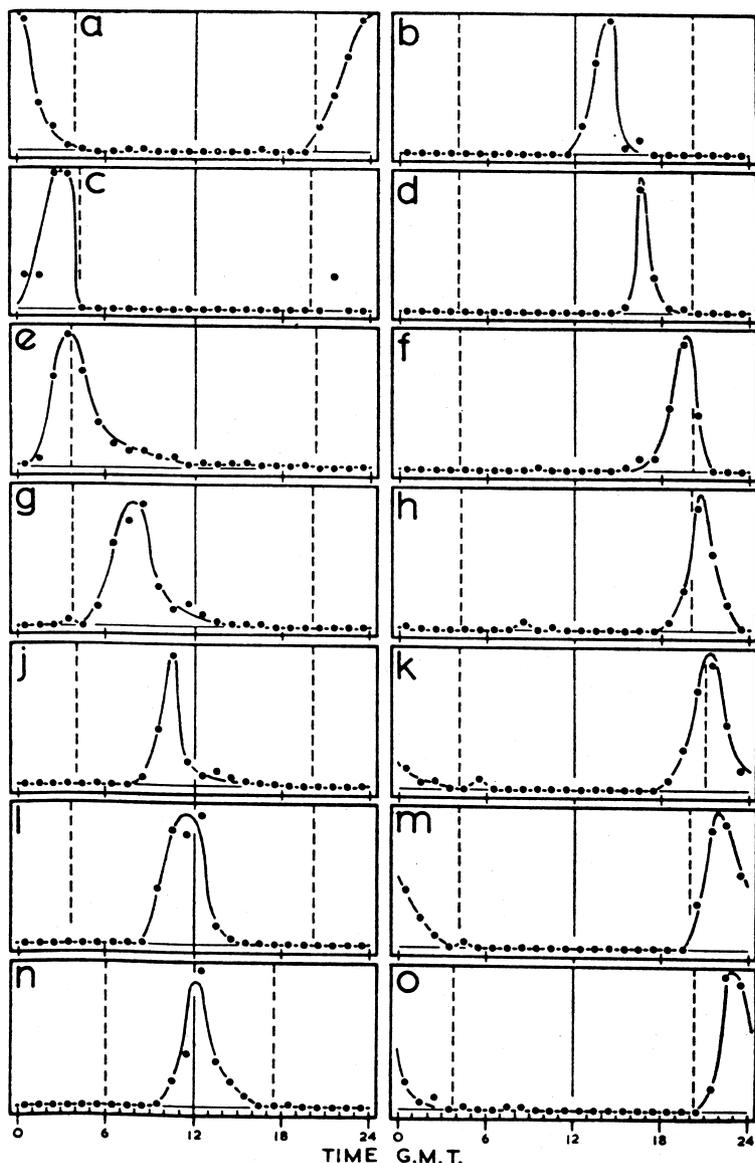


FIG. 6.—Periodicity curves illustrating flight of various insects at all times of the day and night. (a) *Crambus perlellus* (Crambidae: Lep.); (b) *Oligota* sp. (Staphylinidae: Col.); (c) *Celaena secalis* (Caradrinidae: Lep.); (d) *Oxytelus tetracarinus* (Staphylinidae: Col.); (e) *Neuroterus quercus-baccarum*, 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) *Phylloreta 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

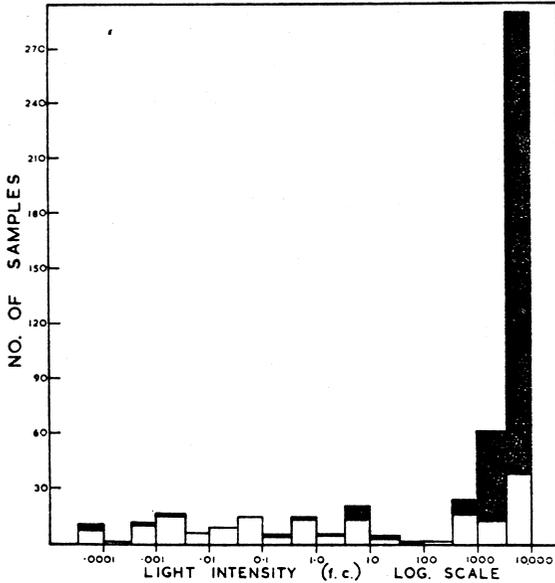


FIG. 7.—The distribution of the mean times of flight in relation to light intensity. Nematocera, Trichoptera and Lepidoptera fly at all light intensities (unshaded areas) but the other insect species (shaded area) fly mainly in bright sunlight.

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.

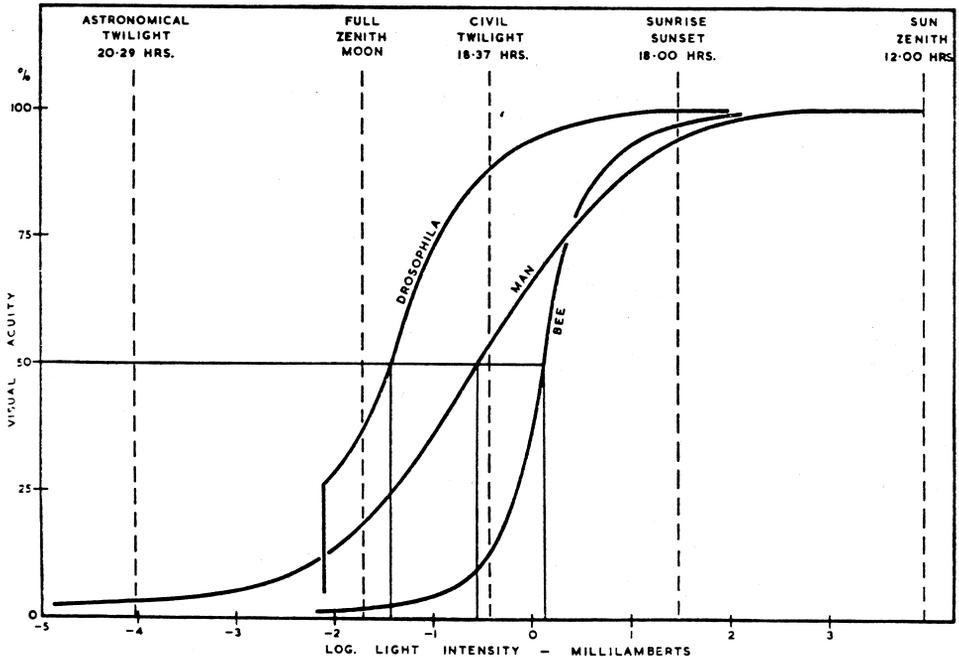


FIG. 8.—Relative efficiency of visual acuity in relation to light and time in man, *Apis* and *Drosophila*.

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.² = 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./cm²/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 & Syrjamaki, 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.

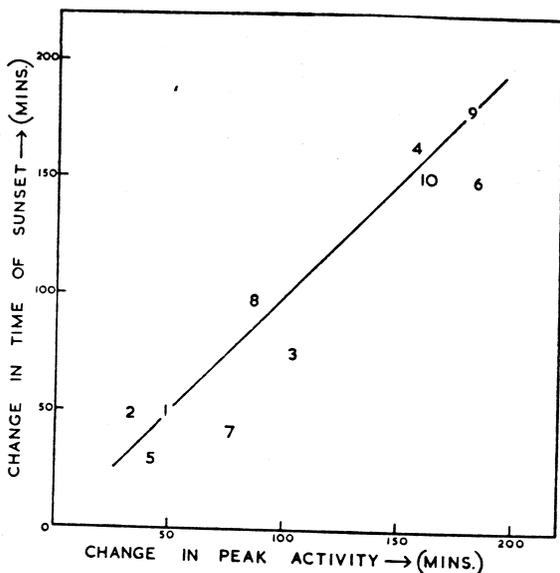


FIG. 9.—Changes in the time of peak activity related to changes in the time of sunset. (1) *Crambus culmellus* (Crambidae: Lep.); (2) *Plutella maculipennis* (Plutellidae: Lep.); (3) *Atomaria lewisi* (Cryptophagidae: Col.); (4) *Limonia nubeculosa* (Tipulidae: Dipt.); (5) *Trichocera annulata* (Trichoceridae: 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 *Kimminsia 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).

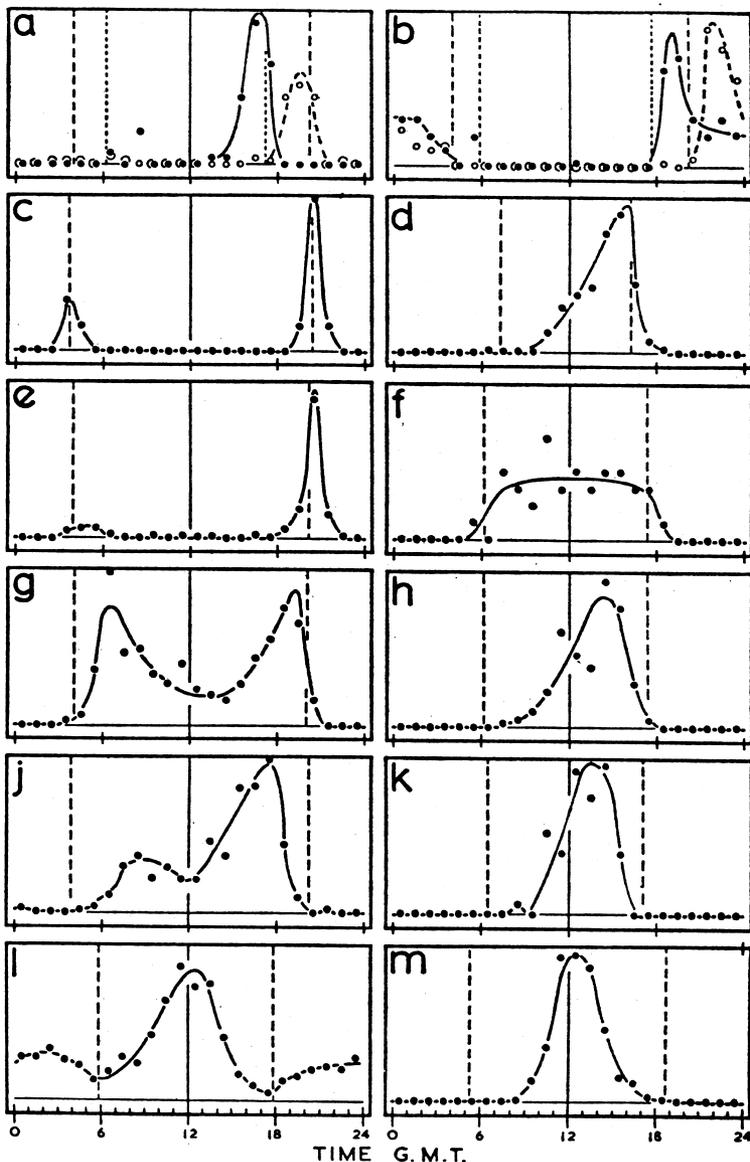


FIG. 10.—Seasonal changes in periodicity curves. (a) *Mycetophila ocellus* (Mycetophilidae: Dipt.): ○ in July, ● in October. (b) *Kimminsia subnebulosa* (Hemerobiidae: Neuropt.): ○ in July & Aug., ● in Sept. & Oct. (c) *Anisopus fenestralis* (Anisopidae: Dipt.) in June. (d) *Anisopus fenestralis* (Anisopidae: 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 prolella* (Aleyrodidae: Hem.) in September. (m) *Aleyrodes prolella* (Aleyrodidae: Hem.) in October.

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. *Phylldromia 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, Ephydridae, 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. *Cnemacantha 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