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# Diurnal activity patterns in hoverflies (Diptera, Syrphidae)

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ABSTRACT. 1. Time-budgets are constructed from censuses of hoverflies. Larger species spend less time in flight.

2. Most species are active under similar conditions of light intensity, but a shade-tolerant (*Melanostoma scalare* Fabr.) and a sun-loving species (*Metasyrphus corollae* Fabr.) were identified.

3. Large species become active (i.e. move, by flying or feeding) at lower temperatures than small ones, except *M.scalare,* which is tolerant to cool temperatures. This means that, *M.scalare* apart, the order of species appearing during the day is size-dependent, largest first.

4. Previous claims about the diel periodicity of syrphids can be reconciled by considering the importance of individual thermal balance.

5. Tolerance to low temperatures in small hoverflies is associated with feeding on anemophilous pollen; this may indicate a proline-fuelled flight.

**Key words.** Syrphidae, thermoregulation, diurnal periodicity, activity patterns, body size.

## Introduction

The periodicity of insect activity is influenced by both endogenous and exogenous factors. Exogenous factors are principally light intensity, temperature, humidity, and wind velocity, and these often appear to act by imposing thresholds which limit the duration of the activity (Corbet, 1966). It is the microclimatic variation of these factors that insects experience (see Willmer, 1982a, b). Lewis & Taylor (1964) concluded that the timing of flight activity in insects is affected by light intensity, whereas the amplitude (numbers seen) is influenced by temperature. Willmer (1983) showed that the temporal appearance of flower-feeding flies is determined primarily by their size and colour, acting through thermal balance.

Hoverflies have been caught in some numbers in light traps at night (Audcent, 1950; Osborne, 1956; Timms, 1956; Birkett, 1959), but Parmenter (1953) examined many thousands of Diptera from a light trap collection and found no syrphids. Grosser (1979) recorded no catches in yellow traps at night. Crepuscular flower-visiting activity is known in at least one hoverfly, *Copestylum vesicularium* Curran, that visits flowers of *Cephalanthus occidentalis* L. around sunrise (Maier & Waldbauer, 1979) and after sunset (Waldbauer, 1963). Grosser & Klapperstück (1977) record syrphids flying into yellow traps at twilight. It seems safe to conclude that, in general, night-active syrphids are simply attracted to light,

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rather than demonstrating true activity (Grosser, 1979).

Here I investigate some factors influencing the diurnal activity patterns of hoverflies, and in particular the temporal sequence of species during the day.

## Materials and Methods

Data were obtained from standard census walks (Pollard, 1977) taken in two garden sites (see Gilbert, 1981b) in Cambridge. The walks were done at weekly or fortnightly intervals irrespective of weather, from early April to early October, 1979. On each census day the route was walked slowly and continuously, usually from just before sunrise to about 16.00 hours BST. Censuses finished at 16.00 hours BST because the density of flies was so low (often fewer than five per hour) as to waste further effort; later times during the day were continually checked throughout the season. Searching *en route* was confined to the immediate semi-circular area ahead, some 3 m in radius. Each hoverfly seen was closely observed for a few seconds, identified, and its activity at the moment of first sight recorded. There were three classes of activity, namely feeding, resting, and flying. Nearly all common syrphids of the sites could be identified in the field without capture (see Gilbert, 1981a). Nomenclature and order of species largely follow Stubbs & Falk (1983).

With each observation I recorded the dry-and-wet bulb temperatures of a pair of hand-held thermometers (held close to the point at which the fly was first seen), the time (BST), cloud-cover on a nine-point scale (0–8), and whether the insect was in the sun or shade. Light intensity was not recorded using a photoelectric method because of the restricted wavelengths generally measured by such devices (Unwin, 1980). Light intensity was therefore estimated from cloud-cover and the sun/shade distinction. Humidities were calculated from the empirical relation given in Unwin (1980). Weighted averages were calculated from the equation

$$\sum_i n_i(i+1)/N,$$

where $n_i$ is the number of observations in category $i$, and $N$ is the total number seen over all categories. This equation calculates an average cloud-cover, for instance, weighted by the frequency of occurrence of flies seen in each cloud-cover category. Statistics were calculated using the original numbers.

These activity data were used to construct crude time-budgets, from the proportion of individuals seen performing each activity. It seems possible that resting individuals are less likely to be observed than individuals flying or feeding. I therefore checked whether these time-budgets were reasonably realistic by following small, dark hoverflies, individual female *Melanostoma scalare,* and recording their activities over 30–60-min periods. The time-budget constructed from these data is close to the census estimate (see Gilbert, 1981a).

## Results

Overall, 7792 individuals of fifty-five species were recorded. The most common by far was *Episyrphus balteatus,* forming 34.1% of all observations. Syrphid abundance during August and early September was very high, those dates containing 79% of all individuals recorded during the year. Apart from time-budgets ($n$=17 species), the results reported here are restricted to the nine commonest species.

### *Time-budgets*

Time-budgets for the seventeen species seen more than fifty times are shown in Table 1. Generally, most time is spent feeding, but resting is also, in terms of time, an important activity. Differences in feeding-time allocation to nectar and pollen feeding lead to the occurrence of a spectrum from pollen specialists to mainly nectar-feeders (Gilbert, 1981b, 1985). Here I would emphasize that there is a significant negative correlation (Fig. 1) between $\log_{10}$ thoracic width and the angular transform of the percentage of time spent flying ($r=-0.61$, $n$=17, $P<0.01$), but no similar significant correlation with time spent feeding or resting. Larger species thus spend less time flying, which may indicate that energy is a scarce resource.

Females spent more time feeding than males

TABLE 1. Time budgets estimated from the numbers of observations in each category during the census walks. Thorax widths are in mm.

| Species | Percentage of time spent: | | | Thorax width | No. of observations |
|---|---|---|---|---|---|
| | Feeding | Resting | Flying | | |
| *Syrphus ribesii* L. | 36.8 | 33.4 | 25.6 | 2.97 | 1160 |
| *Metasyrphus corollae* Fabr. | 66.9 | 18.8 | 4.1 | 2.28 | 803 |
| *Episyrphus balteatus* deG. | 63.7 | 16.6 | 16.4 | 2.45 | 2301 |
| *Sphaerophoria scripta* L. | 67.4 | 21.7 | 8.7 | 1.66 | 92 |
| *Melanostoma mellinum* L. | 42.8 | 31.1 | 23.7 | 1.53 | 283 |
| *Melanostoma scalare* Fabr. | 46.6 | 22.1 | 30.2 | 1.62 | 905 |
| *Platycheirus albimanus* Fabr. | 72.1 | 9.6 | 15.0 | 1.77 | 488 |
| *Platycheirus clypeatus* Mg. | 15.8 | 28.3 | 54.7 | 1.65 | 247 |
| *Platycheirus manicatus* Mg. | 21.8 | 8.4 | 69.5 | 2.08 | 262 |
| *Platycheirus peltatus* Mg. | 48.4 | 13.1 | 37.7 | 2.09 | 122 |
| *Xylota segnis* L. | 96.8 | 3.2 | 0.0 | 2.33 | 94 |
| *Syritta pipiens* L. | 31.4 | 7.8 | 57.5 | 1.68 | 449 |
| *Helophilus pendulus* L. | 52.9 | 45.1 | 2.0 | 3.05 | 51 |
| *Eristalis arbustorum* L. | 84.5 | 10.2 | 2.9 | 3.12 | 206 |
| *Eristalis pertinax* Scop. | 73.7 | 13.7 | 7.5 | 3.84 | 80 |
| *Eristalis tenax* L. | 79.3 | 13.1 | 0.6 | 4.22 | 314 |
| *Myiatropa florea* L. | 39.5 | 59.2 | 1.3 | 3.66 | 76 |

(Wilcoxon signed-rank statistic $T=5$, $n=8$, $P<0.05$). There were some minor inter-site differences in time allocation. Generally species spent less time feeding in the site with fewer flowers, and this same site was also used as a mating site by male *Syrphus ribesii* (Gilbert, 1984) and *E.balteatus*.

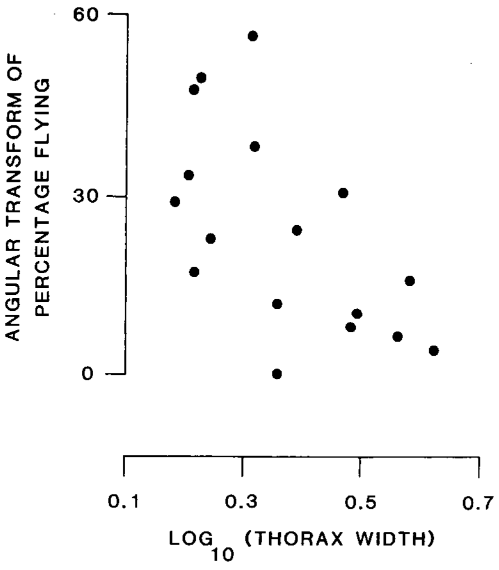

FIG. 1. Correlation between $\log_{10}$ (thorax width) and the angular transform of the proportion of time spent flying, for seventeen hoverfly species.

### *Time of day*

Peak numbers occurred before noon, declining rapidly in the early afternoon. By 15.00 hours BST few hoverflies were seen in the study sites (see Methods). In terms of activities, a typical diel activity profile is shown in Fig. 2; data for others species are similar, but dietary differences occur (Gilbert, 1981b).

Early morning feeding was always on pollen. The incidence of nectar feeding increased to a peak near midday, but pollen was taken throughout the period of syrphid activity. On hot days the taking of water was observed near midday in some species.

It seems doubtful that syrphids measure the time-of-day since days vary in length, and thus combining data from spring, summer and early autumn is probably not a valid procedure. Flies are more likely to respond to climatic factors; I thus reorganized the same data by weather variables.

### *Light intensity*

The average weighted cloud-cover (see Methods) for all observations was 3.55. Most individual species of the nine commonest species have similar averages (from 3.00 to 3.93), except *Melanostoma scalare* (5.91) and *Metasyrphus corollae* (1.70). The overall species × cloud-cover categories table showed

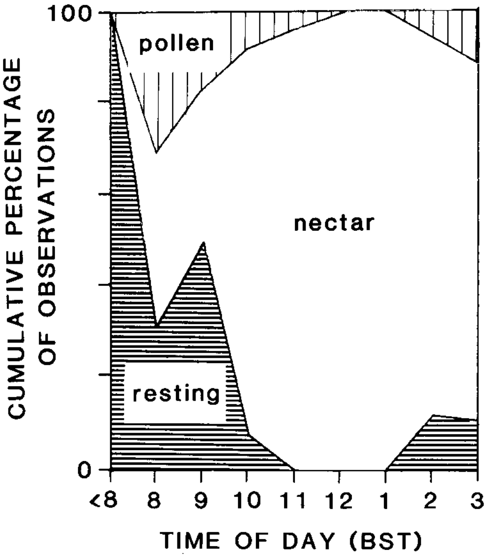

FIG. 2. A diel activity profile for male *Eristalis tenax*. Data have been converted into the cumulative percentage of observations during each census hour. 'Nectar' and 'pollen' refer to flies feeding on these food sources.

significant heterogeneity ($G=1490.6$, d.f.$=64$, $P\leqslant 0.001$) with no non-significant subsets of species (see Sokal & Rohlf, 1969, p. 703). When the distribution of observations for each of the nine commonest species was tested against that for all observations, every one showed significant differences ($G>36.5$, d.f.$=8$, $P<0.001$) except *Eristalis tenax* ($G=8.9$, d.f.$=8$, n.s.). $G$-values for *Met.corollae* and *M.scalare* were an order of magnitude greater than those for the other species (504.3 and 475.2 respectively), and inspection of the details of the calculation shows that the former has a distribution towards low values of cloud-cover, whereas the latter has a distribution towards high values of cloud-cover. Thus *M.scalare* remains active even under complete cloud-cover, whereas *Met.corollae* is a creature of the sun, appearing only when cloud-cover is low.

These patterns were repeated in terms of whether the individual insects themselves were active when the sun was shining on their bodies or not (Table 2). Several species were significantly more likely to be seen in the sun than in the shade when compared with the overall pattern (*Met.corollae, Platycheirus albimanus, Syritta pipiens, Er.arbustorum, Er.tenax*); others were significantly more often seen in the shaded portion of the habitat (*S.ribesii, M.mellinum, M.scalare*). The distribution of observations of *E.balteatus* was not significantly different from the overall pattern. $G$-values calculated from Table 2 are especially high for *Met.corollae* ($G=302.4$, 1 d.f., $P\leqslant 0.001$) and *M.scalare* ($G=286.4$, 1 d.f., $P\leqslant 0.001$), confirming the interpretation from the cloud-cover data above.

Compared with the distribution of all observations for each species, feeding occurred significantly more often from flowers in the sun than in the shade ($P<0.001$ in seven of the nine species), especially for nectar feeding.

Males of all species flew equally in the sun or shade, but females flew mostly in shaded airspace. Females normally flew short distances between flowers, whereas flight in males was usually part of mate-seeking activities.

TABLE 2. Observations divided according to activity and whether the insect was in the sun (S) or shade (Sha).

| Species | Total | | Pollen | | Nectar | | Resting | | Flying | |
|---|---|---|---|---|---|---|---|---|---|---|
| | S | Sha | S | Sha | S | Sha | S | Sha | S | Sha |
| *S.ribesii* | 640 | 503 | 297 | 124 | 3 | 4 | 146 | 247 | 183 | 119 |
| *Met.corollae* | 654 | 84 | 188 | 18 | 280 | 4 | 106 | 47 | 21 | 12 |
| *E.balteatus* | 1289 | 941 | 858 | 443 | 53 | 11 | 176 | 205 | 131 | 246 |
| *M.mellinum* | 88 | 181 | 50 | 54 | 2 | 0 | 21 | 67 | 4 | 60 |
| *M.scalare* | 200 | 506 | 115 | 206 | 11 | 6 | 52 | 122 | 20 | 170 |
| *P.albimanus* | 274 | 136 | 76 | 55 | 99 | 29 | 16 | 26 | 32 | 21 |
| *Sy.pipiens* | 251 | 134 | 29 | 16 | 56 | 10 | 14 | 15 | 143 | 87 |
| *Er.arbustorum* | 156 | 18 | 14 | 3 | 79 | 12 | 15 | 2 | 3 | 0 |
| *Er.tenax* | 204 | 62 | 8 | 8 | 158 | 43 | 24 | 10 | 1 | 0 |
| All species | 4300 | 2890 | 1748 | 984 | 876 | 163 | 677 | 851 | 670 | 822 |

TABLE 3. The lowest temperature at which species were seen, and the temperature at which more than 50% of flies seen were doing something other than resting. Species are in order of size, largest first (see Table 1).

| Species | Lowest temperature seen (°C) | Temperature at which movement occurs (°C) |
|---|---|---|
| *Er.tenax* | 10 | 11 |
| *S.ribesii* | 10 | 12 |
| *E.balteatus* | 10 | 13 |
| *Met.corollae* | 8 | 14 |
| *P.albimanus* | 11 | 13–16 |
| *M.scalare* | 8 | 13 |
| *M.mellinum* | 9 | 17 |
| *Sy.pipiens* | 15 | 16 |

### *Temperature*

Most observations were between 15 and 25°C, but some individuals were seen at temperatures as low as 8°C. There appear to be species-specific differences in the temperature at which activity commences (Table 3; Fig. 3). The order of species appearing as the temperature increases during the morning reflects size differences, the largest appearing first (Table 3: log-log regression, $x$=thorax width, $y$=temperature at which more than 50% of individuals seen were doing something other than resting: $r=-0.85$, $n=8$, $t=3.95$, $P<0.005$). This correlation is tighter when the shade-tolerant (and cool-temperature-tolerant) *M.scalare* is omitted ($r=-0.97$, $n=7$, $t=8.92$, $P<0.001$).

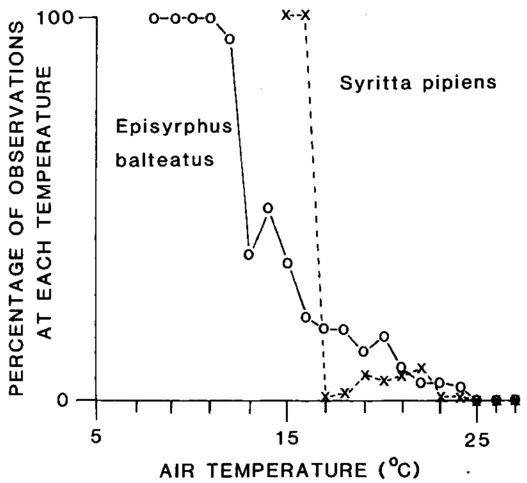

FIG. 3. Percentage of individuals of two species seen resting during the census walks at each degree of ambient temperature.

When observations are further subdivided into separate activities, most individuals were inactive or cleaning below an air temperature of 13°C. Pollen feeding prevailed between 13 and 21°C, whereas the incidence of nectar feeding increased above 20°C. Again, there are species-specific differences. The pollen specialists (*S.ribesii*, *E.balteatus*) started feeding on pollen above 12°C, but only took nectar above 20°C. Nectar-feeders (*Eristalis tenax*) fed on nectar at all temperatures above 11°C. Drinking water normally occurred at higher temperatures only (>21°C).

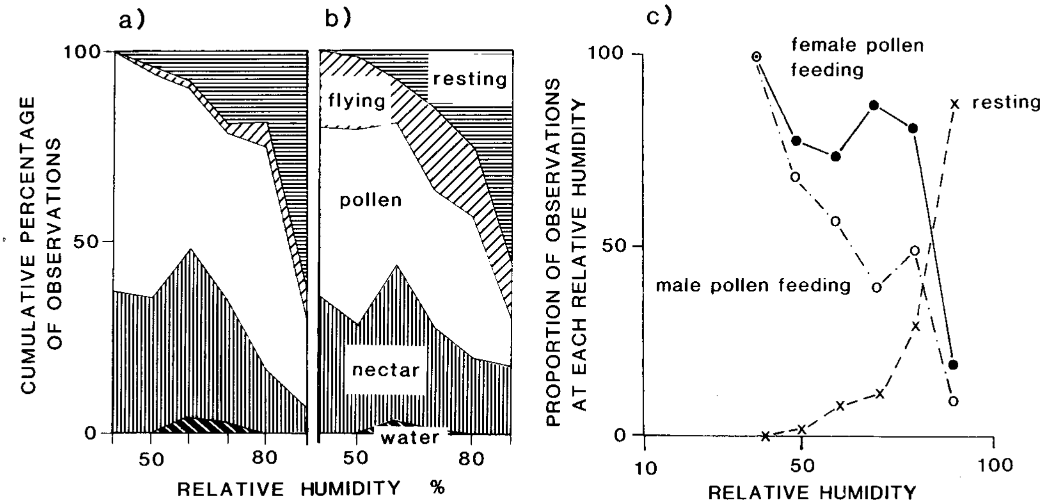

FIG. 4. The cumulative percentage of observations for each category of relative humidity: (a) males of all species combined; (b) females of all species combined; (c) resting and pollen-feeding by *Episyrphus balteatus*.

### *Humidity*

All observations fall between absolute humidities of 5 and 15 mg water $cm^{-3}$ air, and below a vapour-pressure deficit of 21 mbar. Overall, nectar and pollen collection increased as r.h. decreased, and there is a curvilinear relationship between r.h. and the proportion seen resting (Fig. 4a and b). Water collection occurred at the lowest observed r.h., between 50% and 70%. In *E.balteatus* the females only took nectar at less than 60% r.h.; the proportion of males taking pollen declined almost linearly with increasing r.h., but in females this proportion remained high until a relative humidity of 80% (Fig. 4c). Many profiles for other species are similar.

## Discussion

Willmer (1983) has provided evidence for the view that the interaction between thermal balance and diel rhythmicity is responsible for many of the patterns of insect activity seen in nature. She suggests that body size is an important influence upon thermal balance, and that temporal patterns at lily leaves (Willmer, 1982b) and flowers (Willmer, 1983) can be explained from size, reflectance, and the thermal characteristics of the day (see also Willmer & Unwin, 1981). The results presented here support her conclusions.

Different authors have claimed different diel periodicities for syrphids, with peaks either very early in the morning (Nielsen, 1966, for feeding *Helophilus*; Stelleman & Meeuse, 1976; Grosser, 1979; Morse, 1981), nearer mid-morning (Kormann, 1972; Maier & Waldbauer, 1979, for activity near flowers; Zimina, 1957), at or near midday (Lewis & Taylor, 1964), or late in the afternoon (Zimina, 1957). Kikuchi (1962, 1965b) found a mid-morning peak for the 'dominant' species (Eristalini), but a bimodal pattern for 'subordinate' species (Syrphini) on flowers; the bimodal periodicity of the latter group could be transformed into a unimodal one if the dominant species were excluded from the flower patch. A bimodal periodicity was also found for *Scaeva pyrastri* (Schneider, 1958) coming to artificial flowers in March, but this was caused by a long-distance (up to 5 km) daily circulation between feeding and resting places.

In this study, syrphids had their peak activity around mid-morning. Differences in reported periodicities are undoubtedly due either to different activities being observed, or to climatic factors. Very hot regions or days seem to cause the flies to rest during the hottest parts of the day (Nielsen, 1966; Bańkowska, 1964; Zimina, 1957), or to move to cooler places, such as woods (Maier & Waldbauer, 1979). Midday rests cause a bimodal activity pattern; Zimina (1957) observed that feeding from flowers in the sunshine in late afternoon was characteristic of hoverflies, but this is not my experience. Shifts in activity and spatial position are evidently important. Maier & Waldbauer (1979) and G. E. Rotheray (pers. comm.) report that flies move between feeding sites and woodland areas during the course of the day.

Light intensity has been considered important by many authors (Bańkowska, 1964; Grosser, 1979; Grosser & Klapperstück, 1977; Lewis & Taylor, 1964; Zimina, 1957); its effects have been beautifully demonstrated by Kato (1943) and Kikuchi (1965a). If the sun is shining, *Eristalis tenax* (Kato, 1943) and *Scaeva pyrastri* (Schneider, 1958) can remain active at air temperatures below 5°C, and Kikuchi (1965a) related the abundance of *E.tenax* directly to the readings of a blackened heliothermometer. These results support anecdotal evidence that syrphids can be active at low temperatures, e.g. *Criorhina ranunculi* Panzer was seen feeding at sallow flowers on a 'bitingly cold' day with snow on the ground (Edwards, 1956).

Differences in response to temperature between species have been shown previously (Bańkowska, 1961, 1964), but only in the 'optimum' temperature for activity. Grosser & Klapperstück (1977) found no consistent differences in the response to temperature of *Met.corollae* and *E.balteatus*, but they used yellow traps, that only catch individuals orientating towards yellow. On very hot days, negative correlations between activity and temperature have been reported (Maier & Waldbauer, 1979).

All these patterns are explicable in terms of the thermal balance of individual flies, coupled with a diurnal rhythm of activity that brings foragers to flowers when pollen and/or nectar are produced. Both pollen and nectar are normally produced early in the morning in Northern-temperate flowers (Percival, 1956; Corbet *et al.*, 1979). Reflectance properties of the thoracic cuticle (Willmer & Unwin, 1981) may play an important role in the early-morning thermal balance. The earliest syrphids to commence activity (*Eristalis* and *Melanostoma*) have lower reflectance values than the later-appearing *Episyrphus* (reflectance data from Willmer & Unwin, 1981). Furthermore, several *Syrphus* species show remarkable thermoregulatory abilities for such small insects (Heinrich & Pantle, 1975; Gilbert, 1984; unpublished data), as evidenced by comparisons of the body temperatures recorded for the similar-sized *Musca* (Heinrich, 1981, p. 255) with those for *Syrphus* (Heinrich & Pantle, 1975; Gilbert, 1984).

Willmer & Unwin (1981) concluded that body size was the principal determinant of temperature excess for ectothermic, freshly killed insects; reflectance properties influenced the speed of equilibration. Here I have provided evidence that body size is a potent influence on the lowest temperature at which activity can commence (Table 3), and on the duration of various activities (Fig. 1). Thermal economy is probably the main determinant in structuring diurnal activity patterns of syrphids. The net result is that larger insects can gain access to floral resources earlier in the day than can smaller ones, a particular advantage in the cool days of spring.

Large species spend more time feeding on nectar (Gilbert, 1981a, b, 1985), and less time in flight. These correlations tend to imply that energy economy has been selected in syrphid behaviour.

*Melanostoma* is an interesting genus, since its members specialize in feeding mainly or exclusively on grass pollen (van der Goot & Grabandt, 1970; Gilbert, 1981a, b; Clifford, 1964), which is high in starch and proline (Stanley & Linskens, 1974, p. 133, 154). The body temperature of this species during flight is relatively low (Gilbert, 1984). Other syrphids noted feeding during low temperatures are mostly large species (Kato, 1943; Edwards, 1956). Two other small species have been recorded as being capable of activity at low temperatures, *Toxomerus marginatus* Say (Mesler, 1977) and *Platycheirus monticolus* Nielsen (Nielsen, 1972); both feed from anemophilous flowers (*Plantago* and *Salix* respectively), as in *Melanostoma* here. Proline is a substrate for flight metabolism in *Glossina* and other insects (Bursell, 1975; Kammer & Heinrich, 1978). It would be interesting if the ability to fly in the shade at low ambient temperatures in small flies were related to a proline-fuelled flight.

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