THERMOREGULATION IN SMALL FLIES (*SYRPHUS* SP.): BASKING AND SHIVERING

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SUMMARY

1. Flies of the genus *Syrphus* aggregated at specific sites in the field ('lecks'). Flies at lecks were always capable of 'instant' take-of, even at ambient temperatures of 10 °C or less.

2. The flies regulated their thoracic temperature by a combination of basking and shivering. During hovering flight in sunshine thoracic temperature rose 12–14 °C above the ambient temperature.

3. The flies engaged in frequent brief chases while at the lecks.

4. At an air temperature > 18 °C the flies at the leck remained in hovering flight most of the time.

5. The vibration frequencies of the thorax during shivering and flight ranged from about 100 to 200 Hz at 10–27 °C, though at a given temperature and spike frequency the vibration rate during warm-up was higher than the wing-beat frequency (assumed to be the same as thoracic vibration frequency) during flight.

6. During shivering, but not in flight, there is a tendency for the indirect flight muscles to be activated in synchrony.

INTRODUCTION

Flies of the family Syrphidae are capable of hovering flight and rapid flight. In other insects, particularly large ones, these kinds of flight are usually associated with a high temperature of the muscles in the thorax: this temperature is sometimes regulated (Heinrich, 1974). The flies of the present study were about the same size as houseflies, and should thus encounter energetic difficulties during endothermic thermoregulation because of rapid heat loss due to a large surface to volume ratio. On the basis of external appearance, many syrphid flies mimic hymenopterous insects. To our knowledge, however, thermoregulation in syrphid flies has not been investigated.

Males were observed to aggregate at locations where they remained either in hovering flight, or ready for instant take-off at high speed when perched. Since flights at these locations usually involved pursuit of other flies passing by, a high body temperature could be a direct factor affecting mating success. In this study we examine mechanisms of warm-up in preparation for flight, and some of the behaviour relating to body temperature in the field.

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MATERIALS AND METHODS

Most of the field studies were conducted in January and February 1971, in a canyon on an east-facing slope of Mt Diablo, Contra Costa County, California. During this time frosts were frequent at night, and fog often precluded activity of the insects. The flies were observed only in direct sunlight. Other field studies were conducted in 1974 during May and June in Strawberry Canyon on the Berkeley campus.

Thoracic temperatures of flies in the field were measured with a GC32SM2 Fenwal 'micro-mini-probe' thermistor (having a response time of 0·35 sec for 99 % of the full temperature response), and read to the nearest 0·2 °C from a Yellow Springs Telethermometer. The insects were caught by net as quickly as possible (about 10 sec), grasped with a gloved hand, and pierced with the thermistor.

These measurements of thoracic temperature are subject to sources of error. The flies may begin to change temperature immediately after being captured, and heat may flow from the body into the thermistor and glove during the temperature measurement. The latter was investigated by recording, with implanted thermo-couples, thoracic temperatures of living flies which were then grasped, and their thoracic temperatures measured with a thermistor, as above. In eight such trials the thoracic temperatures measured by thermister were less than the thoracic tempera-tures measured by thermocouple by a mean value of 0·09 °C per °C difference between the latter measurements and the ambient temperature. We therefore conclude that the difference between the thoracic temperatures of live flies and ambient temperature was approximately 10 % greater than that measured in the field with a thermistor.

Thoracic temperatures during warm-up and continuous activity in the laboratory were measured with 46-gauge thermocouples with cotton-insulated leads. Tempera-tures were recorded at approximately 9 sec intervals with a Honeywell multipoint potentiometric recorder. Unlike more robust insects, the flies were usually not endothermic when a thermocouple was inserted into their thorax. The thermocouple used to measure thoracic temperature was therefore applied by contact to the dorsal surface of the thorax, where it was attached and covered with resin. Temperatures recorded by this method were no more than 0·5 °C lower than internal temperatures (as determined with heating and cooling curves of the same fly after it was dead with a second thermocouple implanted in the thorax).

Muscle action potentials were recorded from 12·5 μm stainless steel electrodes insulated with enamel except for the tips. Vibrations of the thorax were recorded using an Empire Model MK1-C stereo cartridge with a 10–30000 Hz frequency response. The muscle action potentials (relative to a reference electrode in the abdomen) and vibrations of the thorax were displayed on a Tektronix oscilloscope screen and photo-graphed with a Grass Model C4-R oscilloscope camera.

The flies were used within about 3 h after their capture in the field. In the interim they were provided with cotton soaked in sugar water. The flies were not anaesthetized prior to implantation of electrodes or attachment of thermocouples.

Table 1. *Patterns of activity at leck*

(Ambient temperature = 11–13·5 °C.)

	$\overline{X}$ (sec)	Range	S.E.	N	% time in flight
Uninterrupted perching (basking)	20·2	1–101	3·1	34*	14
Duration of flights	3·23	1–5·5	2·3	22	

(Ambient temperature = 19–20 °C.)

Uninterrupted perching	Spends most of time hovering in sunshine				
Duration of hovering flights	25·9+	15+–58+	3·8	10†	> 95

* Most bouts of basking were interrupted by chases of other individuals.
† Refers to duration of both hover and chase flights. These are minimum flight times. The termination of none of the flights was observed since it was not possible to visually follow flies except on some of their shorter chases.

RESULTS

A. Behaviour

The flies congregated in the forenoons at certain sunlit sites. Since these gatherings of flies included only males, which chased any small flying objects near them, they will subsequently be called 'lecks' in analogy with mating places of some birds.

The flies at the leck were always ready for take-off, even though ambient temperature (T_A) (measured 1 m above ground) was as low as 9 °C. At such low T_A the flies remained stationary while perched on the ground or on the foliage for an average of 20 sec (Table 1). These bouts of 'basking' were interrupted by chasing other flies passing near: the duration of these flights was on the average only slightly longer than 3 sec (Table 1).

Although the lecks were close to shade, the flies were never observed to land in shade. The flies still remained in areas bathed in sunlight. However, later in the season, when ambient temperatures were near 19 °C, they spent most of their time in hovering flight (Table 1). The flies may have been hovering in the area for many minutes, and the 26 sec average observed was probably more an indication of inability to observe them for longer durations at a particular leck, than of actual flying time. However, regardless of the actual durations of uninterrupted flight, it is clear that the flies spent most of their time perched and basking at T_A near 11 °C, while they spent most of their time at the leck in flight at 20 °C. The hoverers initiated chases on the average of every 8·6 sec (range = 1–21·5 sec, N = 31) at one leck.

B. Thoracic temperature

The observed T_{Th} of 30 perched flies at the leck ranged from 26·0 to 32·5 °C (Fig. 1) while T_A varied from 9 to 20·5 °C. (The actual T_{Th} of a fly with its T_{Th} measured as 30 °C at a T_A of 9 °C, for example, was probably close to 32 °C. See Methods.) Relatively high T_{Th} of flies at low T_A could result, in part, from a high substrate temperature. However, T_{Th} were as independent of the temperature of the substrate (ground and/or leaves on low trees) on which the flies were perched (Fig. 1C) as they were of air temperature 2·5 cm above the substrate (Fig. 1B) and 1 m above ground (Fig. 1A). These results indicate that the flies regulated their thoracic temperature, and that thermoregulation involves more than microhabitat selection.
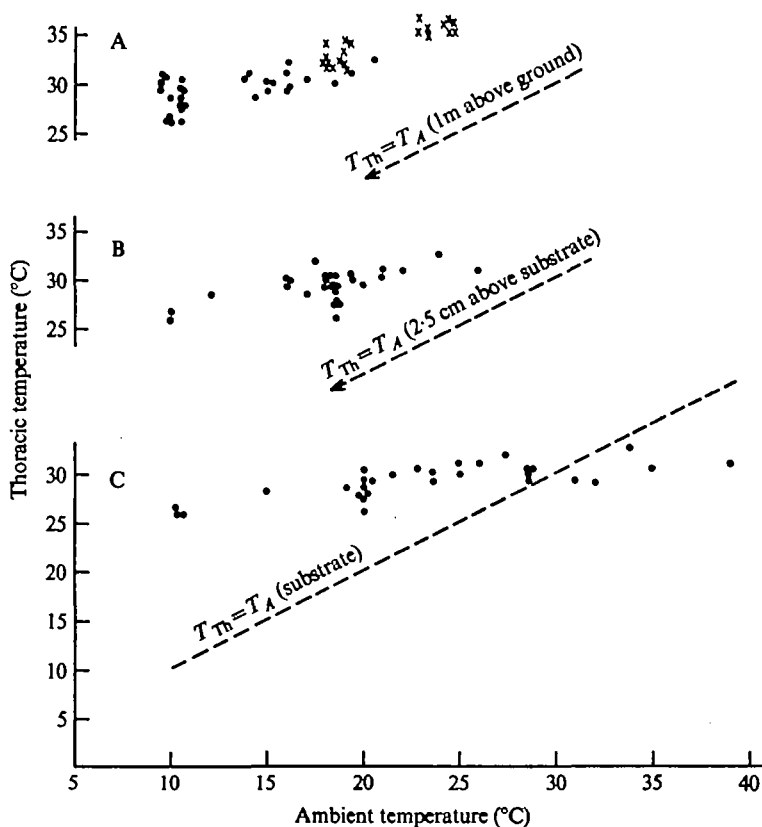
Fig. 1. Thoracic temperature of 30 syrphid flies which had been perching (●) and 12 which had been hovering (×) plotted as a function of: $A = T_A$ 1 m above ground, B = T_A 2·5 cm above ground; and C = substrate temperature. These are the thoracic temperatures as measured. (See Methods for error.)

At T_A of 18–25 °C most of the flies at the leck remained in hovering flight in sunshine. The T_{Th} of these flies ranged from 31·5 to 36·5 °C, averaging 14–12 °C above T_A (Fig. 1A).

At low air temperature many of the perched flies emitted a continuous high-pitched humming. The wings, though folded over the abdomen, were vibrating at a very small amplitude. This suggested that the flies were engaging in endothermic warm-up by shivering.

We examined endothermic warm-up after bringing flies into a thermally uniform environment. Flies freshly caught in the field were placed into a temperature-controlled room and their T_{Th} were measured at several T_A. The flies warmed up but did not maintain their thorax at any specific temperature. The results showed that the flies can be markedly endothermic. A difference of up to 13 °C was observed between T_{Th} and T_A in one fly (Fig. 2) $(T_A = 7·5–10$ °C). The maximum observed difference between T_{Th} and T_A tended to be greater at low T_A than at high, even though T_{Th} always remained less than 28 °C. Periods of endothermy were usually, but not always, accompanied by buzzing and wing vibrations.
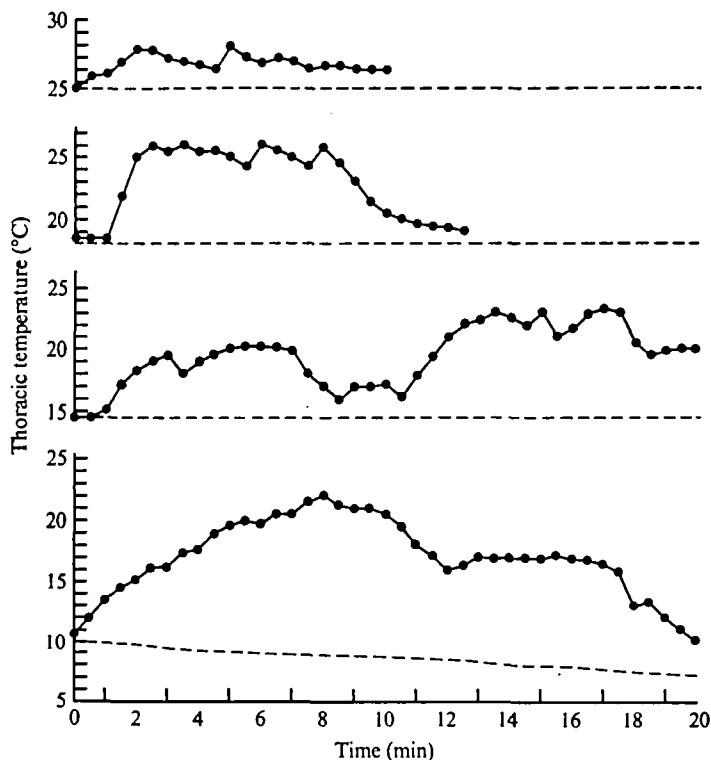
Fig. 2. Thoracic temperatures of a fly tethered by thermocouple leads. The fly was free to walk about. Thoracic temperatures were measured for 10–20 min at ambient temperatures (broken lines) of (from top to bottom) 24·5, 18·0, 14·5 and 7·5–10 °C.
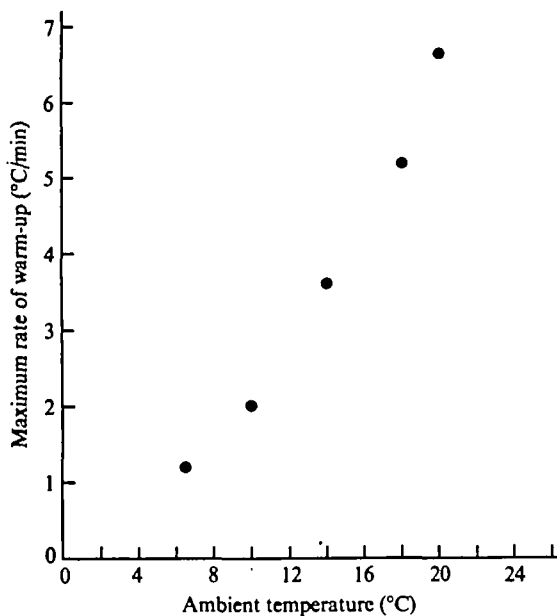

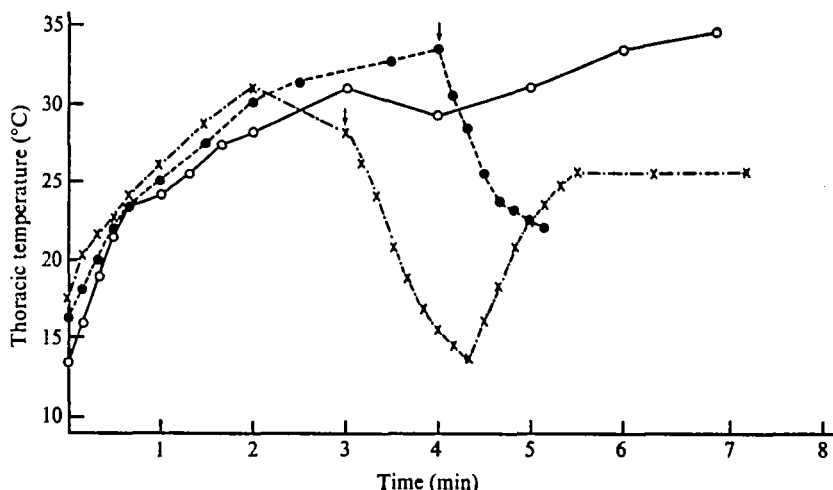Fig. 3. Maximum observed rates of preflight warm-up of a fly at five different ambient temperatures.

Fig. 4. Thoracic temperatures of recently killed flies placed on to the ground in sunshine where they had been basking prior to being caught. Two flies were shaded (at the arrow). The times were 10.20 h ($\times$, ●) and 12.00 h (○), 27 January.
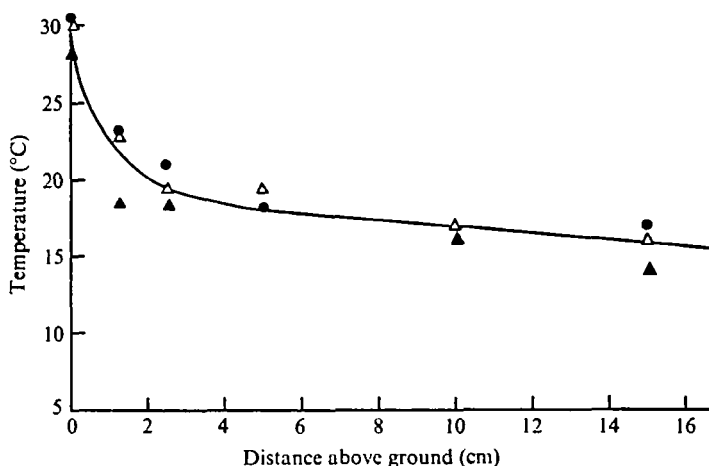

Fig. 5. Profile of air temperature from the ground to 15 cm above it at a leck at 11.00 h (4 February) while the flies were basking in hazy sunshine. Air temperature 1 m above ground = 13·5 °C.

The rate of warm-up varied greatly at any one T_A. However, the maximum rates were dependent upon the ambient temperature, varying from approximately 1·2 °C/min at 6·5 °C, to 6·7 °C at 20 °C (Fig. 3).

C. Thermoregulation by basking

When a shadow was made to fall within 2–3 cm of perched flies they usually remained as if undisturbed. However, as soon as the shadow covered them they flew out of the shade; during 40 instances of such shading, (using the hand at a distance of at least 1 m) flight was initiated in 1 sec or less. The flight into the sunshine was frequently no further than several cm at low T_A, and seldom more than 1 m. At high T_A the flights were of longer duration, but the response was also 'immediate'.
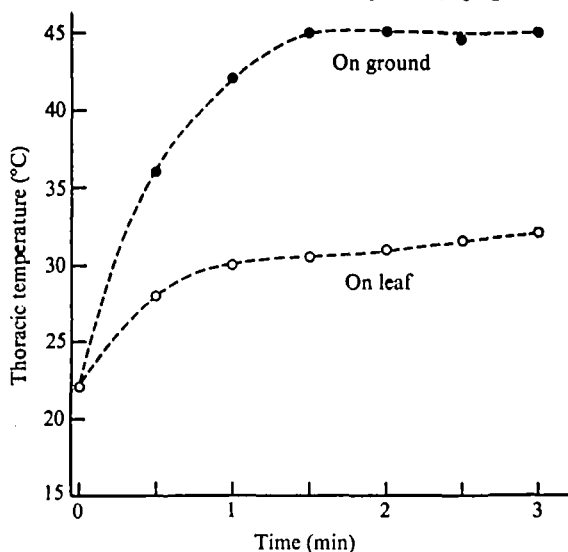
Fig. 6. Thoracic temperature of a dead fly placed on to the ground, and on to a leaf ¼ m above ground. Air temperature 1 m above ground in shade = 23 °C, 5 June. At this time most of the flies were hovering at the leck but a few were perching on the leaves on trees.

The small size of the flies ($\bar{x}$ = 27 mg, 18–40 mg, N = 21) implies a high surface to volume ratio: the microhabitat could thus have a marked effect on their body temperature. When recently killed flies were placed in sunshine on the ground in their leck, they heated to over 30 °C at a rate of approximately 7 °C/min (Fig. 4). However, since the vertical temperature gradient over 2 cm was approximately 10 °C near the ground (Fig. 5), small changes in perch elevation would have a marked effect on their heating and cooling rates. Most flies at low T_A perched directly on the ground. At T_A > 15 °C, however, many also perched on leaves on trees. At T_A near 23 °C most of the flies at the leck were either in hovering flight or perched on leaves. It is probable that they would overheat if they remain perched on the ground, for dead flies placed on to the ground heated to 45 °C in sunshine (Fig. 6). Those ½ metre above ground on leaves on bushes heated only to 30 °C.

D. *Thermoregulation by shivering (warm-up)*

As in the field, flies tethered in the laboratory engaged in warm-up. Warm-up was detected by action potentials recorded from the indirect flight muscles (Figs. 7 and 8), by vibrations of the thorax (detected electronically), by wing vibrations (detected visually), and by increases in T_{Th}. The amplitude of the thoracic vibrations varied, and sometimes the vibrations were detected neither visually nor electronically while the muscles were still being activated (Fig. 7). The thoracic vibration frequency during warm-up was usually higher than the wing-beat frequency during flight (assumed equal to thoracic vibration frequency) at a thoracic temperature of 16 °C. Although wing-beat frequency was nearly independent of the spike frequency recorded from the flight muscles during flight, the vibration rate during warm-up was dependent on spike frequency, but only at spike frequencies < 5 Hz (Fig. 9). At other times no vibrations could be detected although the spike frequency remained high.

Although the effect of temperature on the rate of muscle contractions was not
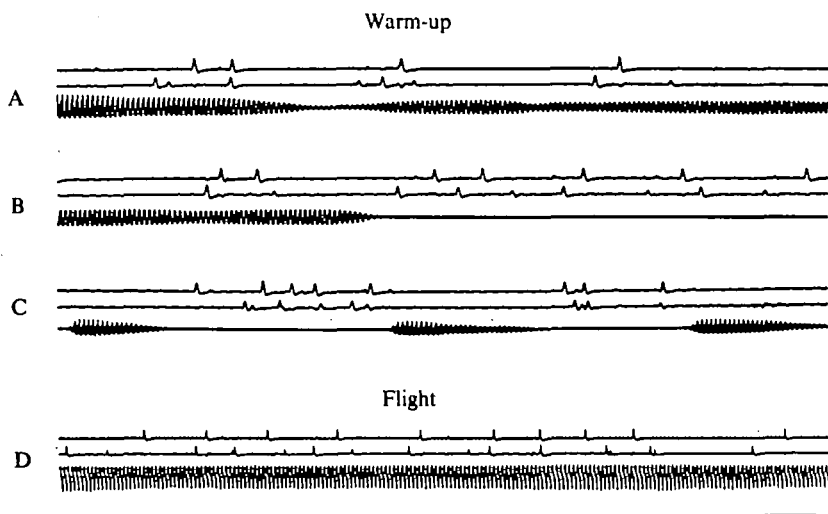
Warm-up

Flight

Fig. 7. Samples of muscle action potentials and vibrations during warm-up (A, B, C) and during tethered flight (D). Each of the four samples were recorded from the same fly with the electrodes in the same position. The upper record of each trace shows the action potentials from the dorsoventral muscle (indirect wing elevators), the middle record shows the action potentials from the dorsal· longitudinal muscle (indirect wing depressors). Note the 'cross-talk' from a neighbouring muscle unit in the lower trace. The bottom line with each set of muscle recordings shows the vibrations of the thorax. The amplitude of thoracic vibration during warm-up is variable and shivering can proceed in the absence of external vibrations. Ambient temperature = 16 °C during warm-up and 25·5 °C during flight. Time mark = 200 msec.
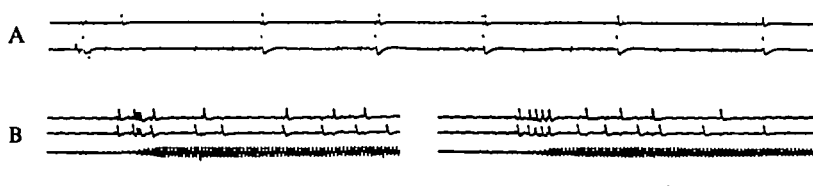

Fig. 8. Examples of activation of two motor units during warm-up (A) and during the initiation of two flights (B). Lowest trace in B indicates vibrations recorded from the thorax. The two recording electrodes were inserted into the right and left sides of the thorax. They were thus probably in the right and left dorsoventral muscles. (The fly pulled free and the location of the electrodes could not be verified.) Time mark = 200 msec.

systematically investigated in the present study, it was clear that oscillations of contractions occurred at relatively low temperatures. The vibration rate of thorax, and hence the rate of muscle contraction during warm-up, was approximately 110 Hz at 10 °C ambient and usually 130–190 Hz at 16 °C ambient.

We wished to know if the patterns of activation of the power-producing muscles of the thorax – the dorsal longitudinal (wing depressors) and the dorso-ventral (wing elevators) – are different in warm-up than in flight, as they are in another myogenic flyer, the bumblebee (Mulloney, 1970; Kammer & Heinrich, 1972). We investigated (1) interspike intervals (Fig. 10) and (2) the phasing of spikes between the dorsal longitudinal and dorso-ventral muscles (Fig. 11) for both warm-up and flight. Interspike intervals during warm-up at 16 °C were usually 25–400 msec. During flight, interspike intervals were shorter and somewhat less variable, usually ranging from
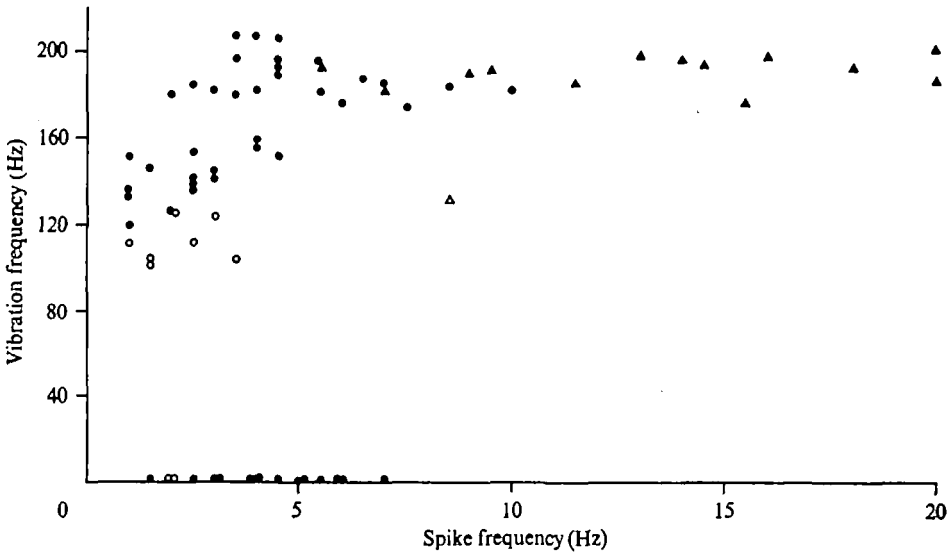
Fig. 9. Rate of thoracic vibrations during warm-up at 15–16 °C (●) and 9–10 °C (○) and flight at 25–27 °C (▲) and 16 °C (△) plotted as a function of spike frequency of one muscle unit of the indirect flight muscles. (When activity of a dorsoventral and a dorsal longitudinal unit were monitored simultaneously, the spikes were added, and the number divided by two.) Muscle spikes and vibrations were counted over 1 second intervals.
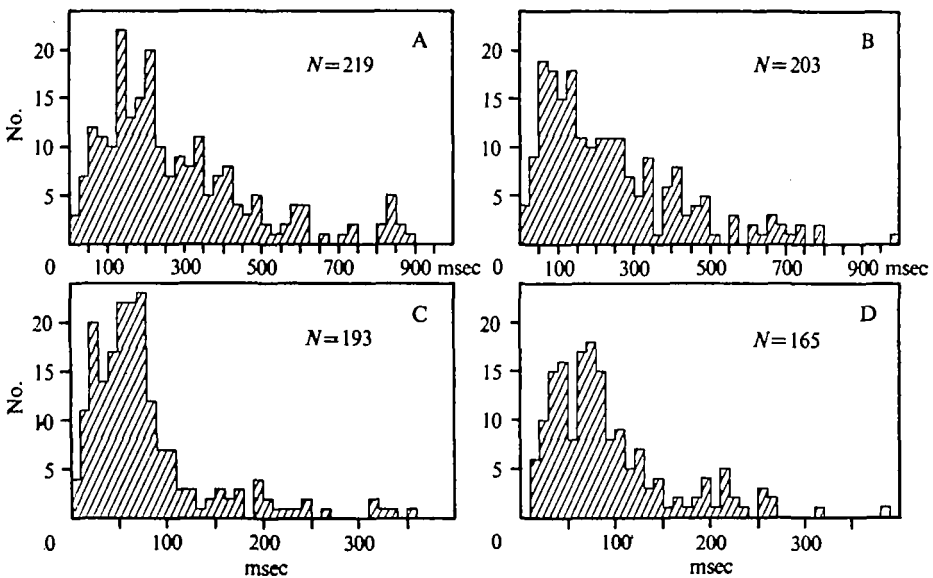

Fig. 10. Interspike intervals during warm-up (A and B) and during flight (C and D). A and C were recorded from a unit of the dorsal longitudinal muscle, C and D represent activity from a single dorsoventral muscle unit. Ambient temperature was 15·5–16 °C during warm-up and 25 °C during flight.
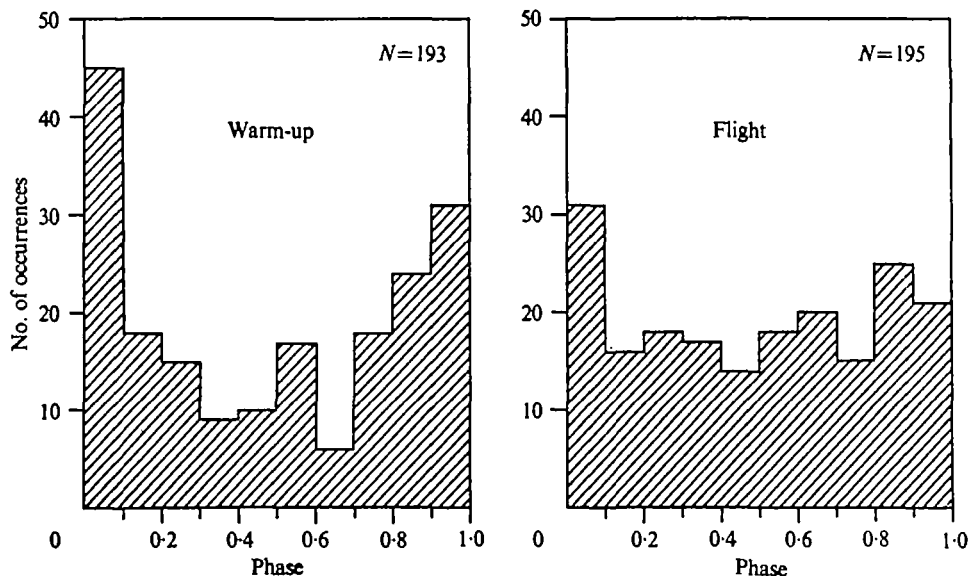
Fig. 11. Phase relationships of a dorsal longitudinal motor unit with respect to a dorsoventral muscle unit during warm-up and during flight. No phase relationship was excluded, but during warm-up there was a tendency for the two motor units to be activated at the same time.

20 to 120 msec (Fig. 10). As is well known for Diptera (Wilson, 1968) there were no phase-preferences during flight. During warm-up, however, there was a tendency for the D.L. and the D.V. (Figs. 7 and 11), and possibly the right and left dorsoventral muscles (Fig. 8) to be activated synchronously, although no phase relationships were excluded.

E. Energetics of endothermy

Unlike social Hymenoptera, the syrphids do not have a large honeystomach in which to transport or store energy reserves. Flies brought into the laboratory usually died in several hours unless they were fed with sugar syrup. Since the flies had no food remaining in the stomach when they died we presumed that they had starved. In order to get an estimate of the fuel reserves that flies carry we examined the flies' crop contents and calculated the energy expenditure required to maintain an elevated T_{Th} by endothermy.

The flies often maintained a difference of 10 °C between thoracic and ambient temperature (Figs. 1 and 2). Based on the cooling rate (8·6 °C/min.) of the thorax (0·0145 g) at such a temperature difference, a fly would have to expend at least 0·1 cal/min (0·8 cal/g °C × 0·0145 g × 8·6 °C/min) if it stabilized its T_{Th} by endothermy. A fly which had fed ad libidum took up 10 mg of 31 % sugar solution. With this amount of sugar the fly should be able to maintain its T_{Th} 10 °C above T_A for 2 h (3·1 mg × 4 cal/mg sugar × 1 min/0·1 cal). Flies caught in the field at their lecks contained considerably less syrup in their crops: the mean crop contents of 21 flies captured at the leck near 11.00 h was 2·4 mg syrup, which contained 41 % sugar. This is sufficient fuel (approximately 1 mg) to maintain a temperature difference of 10 °C by shivering for only 39 min. The flies may thus not remain for long periods of time at the leck since they did not feed there but always maintained a high body temperaturq

Basking, however, could greatly prolong their stay since it could cause large reductions in energy expenditure. Nevertheless, the flies probably need to feed frequently even at relatively high T_A: five of ten flies brought into the laboratory and maintained at 27 °C were dead in 5 h. The remaining five were then allowed to drink water; although they made no further attempts to fly, remaining in torpor, they too were dead the following day.

DISCUSSION

Relatively little is known about thermoregulation in Diptera. In this study we have investigated thermoregulation in small (0.20–0.40 g) syrphid flies, combining field and laboratory observations in order to examine the mechanisms involved and their functional significance.

Previously Digby (1955) observed that the blowfly (*Calliphora*) raised its thoracic temperature 0.75 °C above ambient temperature by endothermy. Hocking & Sharplin (1965) observed mosquitoes (*Aedes*) basking in the flowers of *Dryas integrifolia* in the Arctic, and Edney & Barrass (1962) found that the tsetse fly (*Glossina*) can lower its body temperature as much as 1.6 °C by evaporative cooling when heat stressed while feeding.

Our field studies were restricted primarily to assemblages of males at 'lecks'. Through a combination of basking and shivering, the flies maintain their T_{Th} between 25 and 34 °C at air temperatures (1 m above ground) of 9–21 °C. The maintenance of flight-readiness is often possible only at a relatively great energetic cost. The flies at the leck, although they have the capability to maintain their T_{Th} more than 10 °C above T_A by endothermy, on the average carry only sufficient sugar syrup in the crop to remain endothermic for approximately 40 min. However, they are highly heliotropic and invariably avoid shade. Basking essentially eliminates the need for endothermy under many conditions. Nevertheless, at $T_A > 18$ °C the flies hover in place at the lecks, darting off in brief flights to chase moving objects. We speculate that males with a higher body temperature are favoured in mating success, for these are probably the most rapid flyers (Heinrich, 1974) and should catch females passing near them.

A selective advantage of hovering, rather than perching and waiting for a prospective mate, may be to give an advantage in time over a competing male in the capture of a passing female.

The small body size (approximately one-third that of a honeybee) and the naked thorax must facilitate heat loss, but they must also facilitate rapid heating in sunshine. In view of the probably high selective pressure for a high thoracic temperature, and the great energetic cost to maintain it, it is not surprising that the flies are highly heliotropic. At low T_A they invariably fly into nearby sunshine in less than a second after being shaded.

Endothermy is probably a reserve mechanism. It permits the flies to warm up in shade in the morning, and it allows them to fly to the leck and to feeding areas. It permits the maintenance of a high T_{Th} if convection is great and if heliothermy is not sufficient to elevate T_{Th}.

The mechanism of shivering in the syrphid flies has some interesting differences from that observed in Hymenoptera. Unlike hymenopterans, the syrphids often vibrate

their wings during warm-up. Bumblebees, however, vibrate their wings and buzz sometimes for a minute or more when disturbed in the nest. Unlike bumblebees (Kammer & Heinrich, 1972), the patterns of action potentials recorded from the indirect flight muscles appear to be similar in warm-up and in flight in that there are usually no bursts of impulses during warm-up. However, like bumblebees the indirect flight muscles tend to be activated synchronously during warm-up and asynchronously during flight.

The vibrations during warm-up result in humming which is audible. We do not know whether or not the humming, or the flight sound, also acts as a signal by which the flies congregate (Downes, 1969), as in mosquitoes (Wigglesworth, 1965).

It has previously been suggested that the muscles of myogenic flyers (particularly (bumblebees) may enter into tetanus during warm-up at low T_A (Heinrich, 1974). In view of the present data for syrphids, this view needs reinterpretation. The flies exhibit rapid thoracic, and hence, muscle vibrations during warm-up even at an ambient temperature of 10 °C.

Thermoregulation in the syrphid flies, the smallest endotherms so far investigated, may offer a tool for additional studies of the flight mechanism of myogenic flyers. It may also give new insights into the evolution of endothermy in insects.

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