

Thermoregulation and the structure of swarms in *Syrphus ribesii* (Syrphidae)

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Male *Syrphus ribesii* L. congregate at 'leks', where they alternate between perching and hovering, according to the environmental conditions. The ability of males to arrive at the lek early in the morning appears to be related to their thermoregulatory abilities, which are a function of body size. The temporal and spatial structure of the lek is related to body size, and females may 'choose' larger males partly on the basis of their thermoregulatory abilities. Flight itself leads to a lowering of thoracic temperature in such small flies, and this effect contributes to the distribution of males at the lek.

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Самцы *Syrphus ribesii* L. агрегируются в "скопления", перед самым началом летной активности в ожидании необходимых внешних условий. Способность самцов концентрироваться в скопления рано утром очевидно определяется их терморегуляционной способностью, которая является функцией размера тела. Временная и пространственная структура скопления зависит от размера тела, и самки могут выбирать более крупных самцов, частично по признаку их терморегуляционных способностей. Полет сам по себе приводит к снижению температуры груди у мелких мух, и этот эффект влияет на распределение самцов в скоплениях.

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1. Introduction

Most insects are regarded as ectotherms, with the major avenues of heat exchange consisting of radiative heat gain and convective heat loss (May 1979). Most if not all relatively large insects, however, produce and retain significant quantities of heat when the flight muscles are operating (Bartholomew 1981), and can be regarded as partly endothermic (Heinrich 1981). The thermal balance of many insects has been shown to be an important determinant of behavioural patterns (Willmer 1981, 1982). Radiative heat gain is influenced by surface area and absorptivity of the cuticle, radiation intensity, the presence or absence of hair, and the colour of the cuticle. Convective heat losses are proportional to some fractional power of wind velocity (Digby 1955, Casey 1981). Body shape is also important: elongate insects such as locusts have lower equilibrium temperatures in sunshine than more spherical insects such as Diptera (Digby 1955). The colour and surface reflectance properties of the integument have an effect on body temperature that is less important than that of body size. However, the speed at which insects attain high body temperatures can be significantly dependent upon reflectance (Willmer 1982, Willmer and Unwin 1981).

Several insects, including '*Syrphus* sp.' (Heinrich and Pantle 1975), prepare for flight by activating the flight muscles without allowing the wings to beat.

The regulation of body temperature is accomplished, in the majority of insects, primarily by a variety of behavioural methods, detailed in May (1979) and Casey (1981). Syrphids appear to constitute no exception to this general rule (Heinrich and Pantle 1975, Maier and Waldbauer 1979a,b, Gilbert 1981). Hygrothermal stress is used as an explanation for the switch between mating strategies observed in *Mallota posticata* F. and *Somula decora* Macq. (Maier and Waldbauer 1979b). Here I try to suggest how thermoregulation and mating success may be correlated in *Syrphus ribesii* L., and thereby try to explain some aspects of swarming behaviour of this and other syrphids (see Gruhl 1924).

Male *S. ribesii* congregate in specific locations, usually under trees where there are fairly clear air spaces. These locations are more or less constant in time and space. Males are present from dawn to early evening. These places have been called 'leks' (Heinrich and Pantle 1975), without intending to imply the presence of a dominance hierarchy or territoriality. Males alternate between two behavioural strategies: either they sit on exposed leaves and fly out at passing insects, or they hover in groups, often in shafts of sunlight.

Downes (1969) noted that copulation frequencies in Dipteran swarms are often reported as being very low, and that many observers had seen no matings. No matings were seen in swarms of *S. ribesii*, *Episyrphus balteatus* Degeer, or any other swarming species, during the course of this study. The exceedingly rapid chasing flight of males is very difficult to follow. Bombošch

(1957), Bänšch (1964), and Adashkevich and Karelin (1972) state that copulation in *S. ribesii* is very rapid, a few seconds at most, and in captivity takes place during flight. Where swarming has an established function in Diptera, it is universally reproductive, serving at least as an encounter site for the sexes. Thus although I saw no matings, here I assume a reproductive function for *S. ribesii* swarms.

2. Materials and methods

All experiments were carried out in the Fellows' Garden of St. John's College, Cambridge, during May 1980. Body temperatures were measured using the grab-and-jab technique of Heinrich and Pantle (1975), the thermocouple being inserted into the thorax. All determinations were taken within ten seconds of capture, minimizing heat loss (see Heinrich and Pantle 1975). Individuals were stabbed while held down (still in the net) over a piece of polystyrene.

A sample of ten males was taken from the swarm every hour where possible, throughout the day (14 May 1980) from sunrise to sunset. Each male was dissected, and 14 morphometric variables measured (for details see Gilbert 1981). Times are given in British Standard Time (BST).

Cooling constants, defined as the rate of decline of body temperature per degree excess of the body over ambient (units = per time) were determined according to the method of May (1976). Basically I fastened each fly to a wire with wax, leaving them free to run on a cotton ball. They were then heated in a sealed jar at 100% relative humidity with a microscope light until the thoracic temperature had reached 32–35°C. The light was then removed and the time-course of passive cooling followed. I recorded thoracic temperatures using a small thermocouple (46-gauge) either embedded (large species) or adpressed to the surface (small species) of the thorax.

I marked flies using quick-drying paint applied with a sharpened matchstick to the mesonotum. Three release methods were used: immediate release after marking without anaesthetic; immediate release after marking while the flies were narcotized with CO₂; and release at night by placing opened cages in the lek at 2100 BST.

3. Results

3.1. Male swarming behaviour

Fig. 1 shows the activity of males through the day. Males switch just after midday from perching to hovering. Environmental factors such as temperature are probably responsible for the switch: Fig. 2 shows the same data organised with respect to ambient temperature. Perching was commoner in the shade (62% of

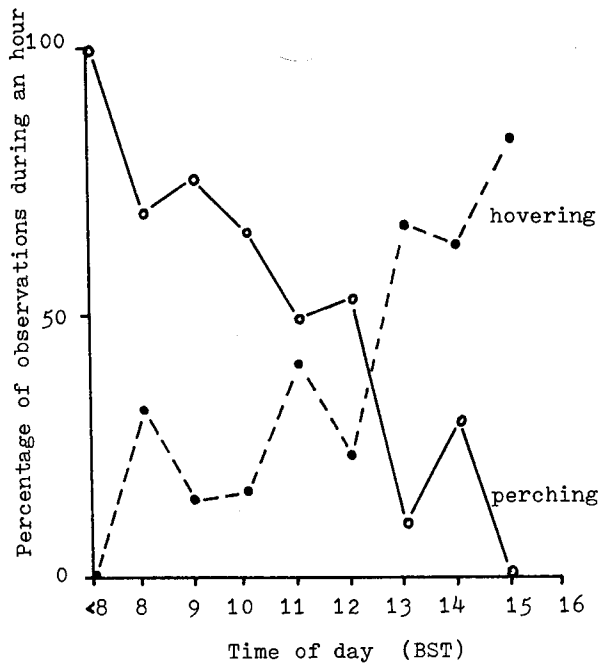


Fig. 1. The frequency of the two mate-searching strategies employed by male *Syrphus ribesii* as a function of the time of day.

perching flies), whereas hovering predominated in the sun (63% of hovering flies).

Only five of more than 450 marked flies were resighted. This implies a continual flux of individuals arriving at and leaving the lek, or that the marking process disrupted residence. From energetic considerations, the former is plausible (see below).

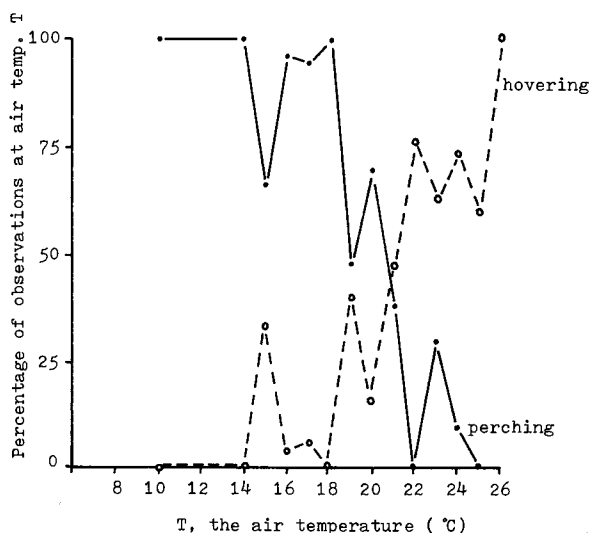


Fig. 2. The same data as for Fig. 1 plotted as a function of the ambient temperature.

Tab. 1. The crop contents of male *Syrphus ribesii* caught in 'leks'.

Crop volume (µl)	Maximum = 6.0
	Mean = 1.67 ± 1.34 (n=96)
Crop sugar (mg sucrose equivalents)	Maximum = 4.97
	Mean = 1.37 ± 1.12 (n=96)
Concentration (% sucrose equivalents)	Maximum = 71.0
	Mean = 63.16 ± 3.90 (n=93)

Males hovering in the middle of the air space of the lek will normally settle upon a perch if one is offered. Since these individuals do not move to the nearest natural perch, I infer that position is in some way important.

Swarming affects male foraging behaviour. Males with no or very little sperm in their testes were not present in the lek, but fed on pollen from flowers (see Gilbert 1981). Males from the lek invariably have few (<50) or no pollen grains in the crop. The concentration of crop contents was remarkably uniform and high (Tab. 1), and led me to suspect that refractile substances other than sugars might be present. The testing of the hypothesis that only simple sugars were present involved two independent methods. First, I used thin-layer chromatography with Gelman plates and a CCl_4 - methanol solvent; secondly, the freezing point depression of the crop contents was measured with a field osmometer (Unwin and Willmer 1978) and compared against reference curves for pure sugars. Both methods indicated that, far from being contaminated by other substances, the crop fluid was an exceptionally pure mixture of sucrose, glucose, and fructose. All the few pollen grains present were rosaceous, probably *Crataegus*. Percival (1961) records *Crataegus* nectar as dominated by fructose and glucose, but with sucrose present too.

Later in the season, male *S. ribesii* usually feed on honeydew, often on *Acer* leaves in early evening when no males are in the lek.

3.2. Body temperatures

Fig. 2 indicates that thermoregulation may be an important determinant of activity, since ambient temperature evidently influences the type of mating behaviour adopted. Perching males emit a note of variable pitch (starting low and ending high) that is clearly audible from several metres.

Results of the 'grab-and-jab' determinations are shown in Fig. 3. The slope of the line is significantly different from unity (product-moment regression), indicating that regulation occurs. Individuals measured while perching are not distributed about the line any differently from hovering ones (17 above, 18 below; $\chi^2 = 0.03$, $P > 0.90$). This also holds true for a comparison

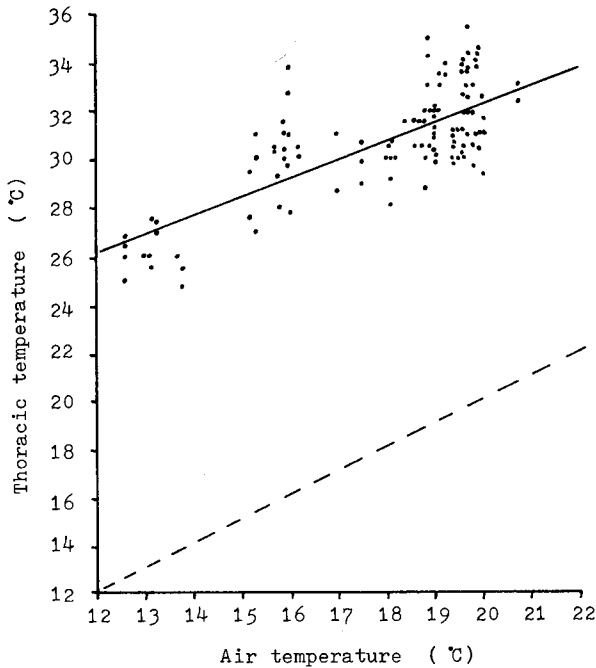


Fig. 3. The thoracic temperatures of male *S. ribesii* in the lek on 14 May, 1980, using the 'grab-and-jab' technique. Correlation, $r = 0.7176$, $n = 111$, $P < 0.0005$. Linear regression, slope = 0.7627 ± 0.1672 (99% confidence limits). Dashed line indicates where body and ambient temperatures are equal.

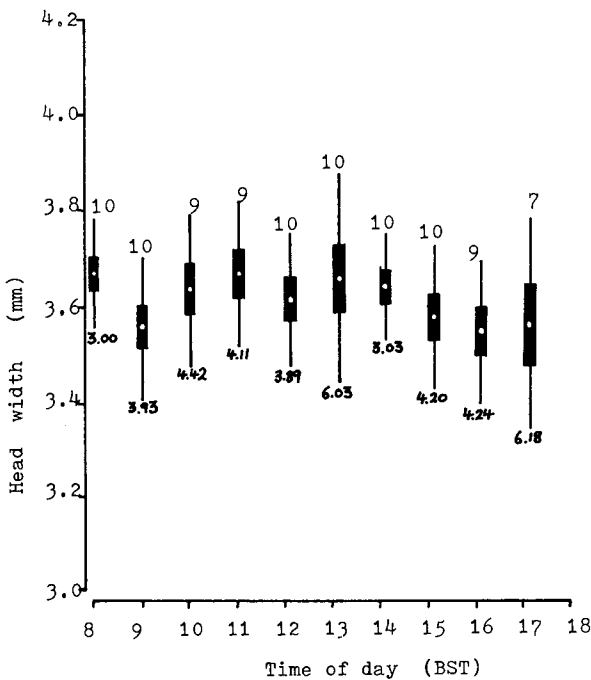


Fig. 4. Head widths of male *S. ribesii* sampled from the lek on 14 May, 1980. Figures above the standard error of the mean boxes and standard deviation bars show the sample sizes, figures below show the coefficients of variation.

of males measured in the shade with those in the sun (6 above, 10 below; binomial probability = 0.244).

3.3. Size variation and crop contents

Head width is more highly correlated with body size than other variables ($r = 0.94$ with PCI: see Gilbert 1981), and is therefore used as an index of body size. Fig. 4 shows the head widths of males in the lek during each hour of the sampling date. Flies caught between 0800 and 0900 BST are significantly larger than those caught during the subsequent hour ($t = 1.95$, d.f. = 1, $P < 0.05$). The samples from other hours do not differ significantly from the first sample. However, the mean of the first sample has the largest value of all sample means, and this sample also has the lowest coefficient of variation (Fig. 4). I interpret these data as indicating that the first arrivals at the lek are all relatively large individuals. No males were seen before 0800 BST.

Amounts of crop sugar are shown in Fig. 5. Males of the first sample have on average more than twice as much as other males. There is a low correlation between crop volume and body size in male *S. ribesii* ($r = 0.22$, $n = 95$, $P < 0.05$: see Gilbert 1981).

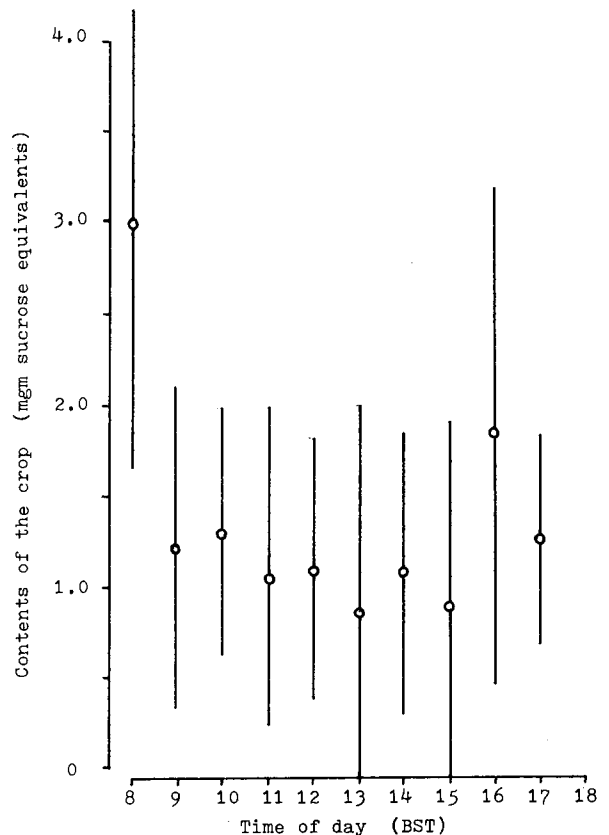


Fig. 5. The amounts of sugar (in sucrose equivalents) in the crops of male *S. ribesii* in the lek on 14 May, 1980; sample sizes as for Fig. 4. Standard deviation bars are shown.

Tab. 2. Analysis of the size of hovering male *Syrphus ribesii* caught in the sun or the shade: head widths of sampled males.

Parameter*	Sun	Shade
N	12	11
Mean	3.2083	3.5664
SD ₁ *	0.4287	0.2005
SD ₂ *	0.0590	0.0258
Variance ratio $F_{11,10}$	= 2.29 (P≈0.10)	
SE of difference	0.1418	
Observed difference	0.3581	
t_{21}	2.52 (P<0.01)	

* Head widths; standard deviations calculated using degrees of freedom, SD₁ refers to raw data, SD₂ to log data. The variance ratio is calculated from log. data.

Two samples were taken on 10 May 1980 between 1200 and 1300 BST (air temp. = 20°C), one of 12 males hovering in the sunshine, and the other of 11 hovering in the shade. Tab. 2 gives the results of comparing head widths. Males caught in the shade were significantly larger.

3.4. Cooling constants

Normally cooling constants are plotted against body size in a double-log plot to give a straight regression line. Here I plot untransformed data (Fig. 6) to emphasize the curvilinearity. The graph demonstrates that, over the range of weights found in male *S. ribesii* (20–45 mg), the rate of loss of heat changes by a factor of more than two. The cooling constant of flies larger than about 40 mg is relatively constant at 0.07–0.09 per 5 s, whereas small *S. ribesii* lose heat more than twice as rapidly.

During these experiments, some flies released the cotton sphere held by their tarsi, and started to fly. Thoracic temperature in these flies declined markedly. The effect diminishes as body size increases towards the

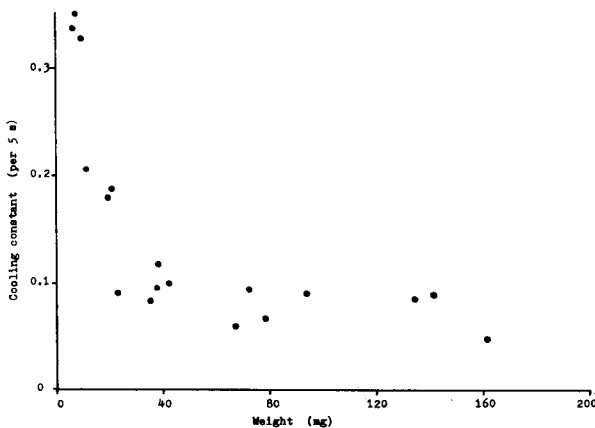


Fig. 6. The cooling constants of several species of syrphid plotted against body weight.

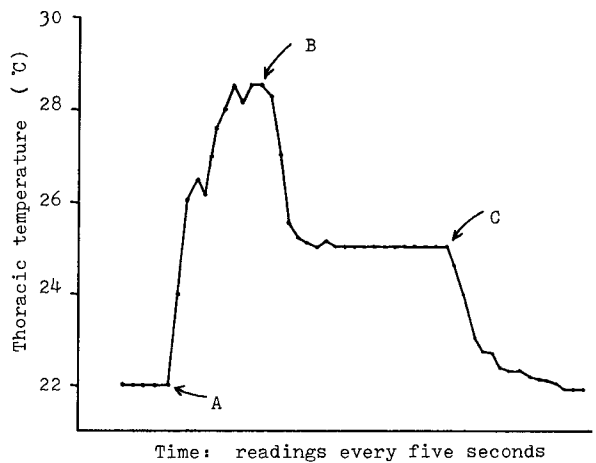


Fig. 7. Thoracic temperature of a male *Melanostoma scalare*, showing that flight reduces the thoracic temperature; at A the external heat source was applied; at B the insect started to fly; at C the heat source was removed and a landing platform provided.

largest species, which suffered only small drops in body temperature. Flights usually lasted only a few seconds. In large species continuous flight probably leads to a gradual increase in body temperature (cf. Bartholomew and Heinrich 1973). A few individuals of the small *Melanostoma scalare* F. did fly for longer periods: the time-course of thoracic temperature in one such fly is shown in Fig. 7. It is clear that flight caused a large reduction in thoracic temperature (cf. Heinrich 1972 for *Bombus*).

3.5. The females

Female *S. ribesii* were hardly ever seen at the lek during this study. Those that were seen were only present very early in the morning, before sunrise, resting on leaves at the edge of the lek. The corresponding air temperature was low, a mere 10–12°C. All females caught at these times (n = 4) were dissected. None had any traces of sperm in their spermathecae, and their ovaries were completely undeveloped.

4. Discussion

Activity in *S. ribesii* is strongly influenced by the thermal characteristics of the day. Similar data for other species suggest interesting differences in the temperatures at which activity takes place (Gilbert 1981). For example, while the large *Eristalis tenax* L. is seen at temperatures as low as 10°C, much smaller species such as *Syritta pipiens* L. do not appear until air temperature has reached 15–16°C.

The temporal pattern of the swarm appears to conform to the following pattern. In the very early morning,

before the sun has risen, unmated females emerge from their overnight resting places, possibly at the lek itself. Males arrive soon afterwards, the largest first because air temperature is too low for the smaller flies. At first, males are confined to the perching strategy since energetically it is too expensive to hover. Instead, they maintain flight readiness by warming up, a less expensive behaviour in energetic terms than flight because convective losses are minimised. These early males are confined to perching in sunspots, presumably also for thermoregulatory and energetic reasons.

As air temperature rises, large males are able to remain on 'good' perches whether or not they are in sunspots, but incoming smaller males are probably confined to perches in the sun. Males switch to the hovering strategy, probably as soon as it becomes energetically feasible. Heinrich and Pantle (1975) assumed that hoverers did better because they could reach a passing female more quickly than can perchers. However, since hovering males will usually land if a perch is offered, it is probable that Gruhl's (1924) hypothesis is more likely, i.e. that a central position affords a better view than a perch at the side of the lek. Once again the larger males precede the smaller ones in hovering, at first only in sunshine, but later the hovering position becomes independent of sunspots.

Hoverflies weighing about 40 mg use about 0.013 W during flight (Gilbert 1981). Males caught between 0800 and 0900 hours therefore had enough energy for an hour's use, whereas later males only had enough for about 25 min. The similarity of variances in Fig. 5 implies that the later samples are not simply diluted by males that have been in the lek for some time, and are therefore low on crop sugar. These results are similar to those obtained by Heinrich and Pantle (1975).

It therefore seems likely that males remain in the lek for a relatively short time before they must leave to refill the crop. The first arrivals after dawn have probably spent the night with crops filled the previous evening. Having left, it is unlikely that males return to the same lek site after feeding, resulting in a continual turnover in the identities of individuals at the site.

Females appear to be present at the lek mainly, if not only in the early morning. Is their time of arrival the criterion by which females choose their mates? It is possible that males distribute themselves temporally with the result that reproductive gains are equalized, the temporal equivalent of Fretwell's (1972) "ideal-free distribution". This would suggest a reason why males persist throughout the day, when there are apparently no females.

Large males thus appear to have an advantage. What is the selective force opposing size increase? The usual ad hoc postulate is that larger males take longer to develop as larvae, and take longer to collect sufficient food before returning to the lek. It is therefore interesting that labellum width is more highly correlated with body size in males than females, and the slope of the regres-

sion is significantly higher in males (Gilbert 1981). Males also show strong univariate and multivariate negative skew (Gilbert 1981), indicating that selection may act more strongly against very small individuals than against very large ones. Females show no univariate or multivariate skew.

Heinrich (1981: 250), Casey (1981: 105), and Willmer and Unwin (1981) recognise that the balance between metabolic heat gain and convective heat loss alters with body size, and that the smallest insects do not increase their thoracic temperature due to activity of the flight muscles. The regression line of thoracic against ambient temperature (Fig. 3) is very similar to that obtained by Heinrich and Pantle (1975), and it is possible that the species studied by these authors was *S. ribesii* (B. Heinrich, pers. comm.). The temperature excess is very large for an insect of this size (cf. data for *Musca domestica*, Heinrich 1981: 255). Casey (1981) notes that the thermoregulatory abilities of *Syrphus* are remarkable for so small an insect.

The 'singing' of *S. ribesii* was assumed by Carter (1919) to be an expression of the insect's "joy in life": he could detect no females attracted by the sound. Singing behaviour is known in the Syrphidae from at least *Helophilus*, *Microdon*, *Sericomyia*, and other *Syrphus* species (Carter 1919, Laidlaw 1933, pers. obs.). In other Diptera, *Glossina* and *Gasterophilus* have been noted, and there may be others. The frequency of the sound is linearly related to thorax temperature in *Gasterophilus* (Humphreys and Reynolds 1980), and Heinrich and Pantle (1975) recorded higher frequencies at higher thoracic temperatures in *Syrphus* sp. This provides indirect evidence that flight causes a reduction in thoracic temperature, since singing commences immediately upon landing, and the frequency of the tone is then at its lowest.

In insects as small as many syrphids, flight itself may be a means of keeping cool. This heat loss may also act as a limitation to extended flight, such as hovering in the lek under certain conditions. The decline in temperature is presumably a result of the tremendous convective currents caused by the beating wings.

With constant wind speed and insolation, there is a linear relationship between temperature excess and thorax width for suspended, recently killed Diptera (Fig. 8, Line D; see Digby 1955). When flying Diptera are considered, the two opposing forces of increased convective losses and endothermic gains differ in relative magnitude according to body size, from simple size and shape considerations. Thus we may visualize a situation corresponding to that of line A in Fig. 8 for insects that do not actively thermoregulate. Below a certain size, flight causes the equilibrium body temperature to fall below that achieved by stationary insects. The temperature excess cannot increase indefinitely: a more realistic relationship for body temperature with size is therefore line B of Fig. 8.

The equilibrium temperature is likely to alter with in-

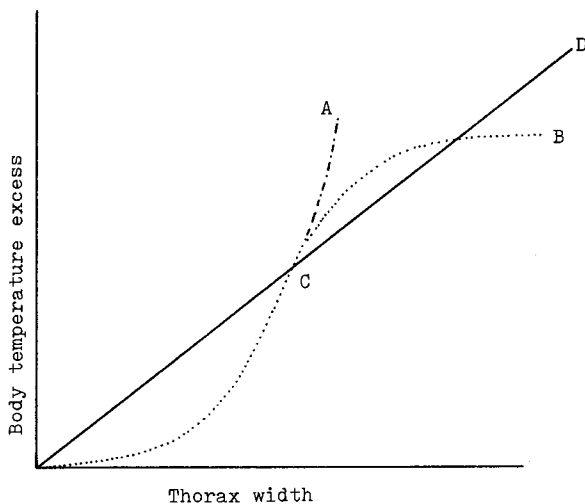


Fig. 8. Hypothetical relationship between the excess thoracic temperature and body size: see text for explanation.

solution, probably in direct proportion (Cena and Clarke 1972). An additional, and less predictable factor, is wind speed. The position of point C in Fig. 8 is therefore uncertain with respect to body size. Humphreys and Reynolds (1980) record an increase in thorax temperature during flight in an 85-mg male *Gasterophilus intestinalis* DeGeer, but also substantial decreases in the same for a 125-mg female. Even large insects may show decreases in thorax temperature under certain circumstances: Heinrich (1972) recorded such a decrease during the tethered flight of a queen *Bombus vosnesenskii* Radoszk. Willmer (pers. comm.) suggests that point C lies between 80 and 100 mg in Diptera.

No fly exhibited any signs of active regulation of the thoracic temperature other than by attempting to walk or fly.

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