

TEMPERATURE REGULATION IN BEE- AND WASP- MIMICKING SYRPHID FLIES

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Accepted 8 May 1987

SUMMARY

1. Thoracic temperatures were measured in 12 syrphid species.
2. During field activity the flies maintained thoracic temperatures near 30°C by a combination of basking and endothermy. In the 10 species which were mimics of Hymenoptera, thoracic temperatures averaged a few degrees below those of their models.
3. All of the syrphids tested demonstrated a marked capacity for endothermic warm-up in the laboratory. Warm-up rates ranged from 1.2–5.5°C min⁻¹. The maximum rate of warm-up increased in a linear fashion with body mass, with a slope of 4.3.
4. The flies sometimes sustained endothermy beyond the 2–5 min necessary for thoracic temperature to reach flight temperature. One individual maintained an average temperature excess of 13.4°C for more than 26 min.
5. Cooling rates were highly dependent on body mass and did not differ significantly between pubescent *Bombus* mimics and glabrous species. Removal of pile from the thorax of *Bombus* mimics increased their cooling rates by about 30%.
6. From the comparisons between wasp and bee mimics, we conclude that although the pubescence of *Bombus*-mimicking flies aids endothermy, it is not necessary to achieve it. Their pubescence has apparently evolved primarily to improve visual mimicry.

INTRODUCTION

Adult syrphid flies (Diptera: Syrphidae) visit flowers to forage for nectar and pollen and to search for mates. Their importance as pollinators is second only to that of bees (Curran, 1934; Kevan & Baker, 1983). Many syrphids are exceptionally accurate visual mimics of aculeate Hymenoptera. Bumblebee mimics are covered with thick pile whereas mimics of vespid wasps and non-mimetic species are glabrous or have relatively sparse pile. In spite of the variety and abundance of Syrphidae, they have not been intensively studied. In particular, the ability of these flies to thermoregulate during activity is poorly understood.

Key words: Diptera, Syrphidae, thermoregulation.

Table 1. *Body masses and presumptive models (if any) of syrphid flies studied*

	Mass (g)	N	Model
<i>Criorhina nigriventris</i> (Walton)	0.207 ± 0.0320	39	<i>Bombus</i>
<i>Mallota posticata</i> (Fab.)	0.162 ± 0.0550	12	<i>Bombus</i>
<i>Sericomyia militaris</i> (Walker)	0.134 ± 0.0326	7	<i>Dolichovespula</i>
<i>Temnostoma alternans</i> (Loew)	0.130 ± 0.0429	53	<i>Vespula</i>
<i>Mallota bautias</i> (Walton)	0.125 ± 0.0326	10	<i>Bombus</i>
<i>Temnostoma vespiforme</i> (L.)	0.122 ± 0.0293	48	<i>Vespula</i>
<i>Erstalis barda</i> (Say)	0.115 ± 0.0468	10	<i>Bombus</i>
<i>Erstalis</i> sp.	0.095 ± 0.0251	22	non-mimetic
<i>Sericomyia lata</i> (Coquillett)	0.093 ± 0.0342	8	non-mimetic
<i>Sericomyia chrysotoxoides</i> (Marquart)	0.086 ± 0.0251	24	<i>Vespula</i>
<i>Sphecomyia vittata</i> (Weid.)	0.085 ± 0.0211	6	<i>Vespula</i>
<i>Chrysotoxum</i> sp.	0.067 ± 0.0362	31	<i>Vespula</i>

Values represent means ± standard deviation.
N is the number of individuals.

Many bees and wasps foraging at the same flowers as syrphid flies maintain high body temperatures during activity, using metabolically generated heat (Heinrich, 1983; Heinrich & Heinrich, 1983). Their endothermy permits some of them to be active at ambient temperatures near 0°C. At our study site the largest syrphids are the same size as the smallest bumblebees and wasps, whereas the smallest are considerably smaller than any previously studied endothermic hymenopteran. We here examine thermoregulation in a variety of syrphid flies and compare thermoregulation in the flies and their hymenopteran models.

MATERIALS AND METHODS

We obtained data on 12 species of syrphids ranging in body mass from 0.05 to 0.33 g (see Table 1 for species names). Most were collected near Weld, Maine, while some *Chrysotoxum* sp. were collected near Richmond, Vermont. The flies were studied from May to August 1985, inclusive, with preliminary data collected during the summer of 1983. Bees and wasps were also collected in Weld. The insects were kept in airtight vials and were weighed (± 0.001 g) within several hours of capture.

Thoracic temperature

We measured thoracic temperatures (T_{th}) in the field using a Sensortek microprobe needle thermocouple (Type MT-2911, time constant = 0.025 s, needle diameter = 0.33 mm). Insects were captured with an aerial net in flight or while perched and the couple was inserted into the centre of the thorax. Measurements were made with the insect immobilized in a pocket of netting to avoid hand contact and to reduce handling time (usually 3–5 s). The thermocouple was dried and air temperature (T_a) was measured in the shade near the site of capture immediately after T_{th} had been measured. Temperatures were read to the nearest 0.1°C on a Sensortek Bat-12

thermocouple thermometer that had been calibrated against a mercury thermometer traceable to the US Bureau of Standards.

Warm-up and sustained endothermy

Syrphid flies for measurements of endothermic warm-up were captured during the afternoon and stored individually at 5°C until they were used the following morning. A thermocouple (0.03 mm in diameter) was inserted through the dorsolateral thoracic cuticle (couple at midthorax) and fixed in place with a drop of melted beeswax. T_a was measured with a temperature-sensitive integrated circuit (LM334) placed near the insect. Outputs of the thermocouple and the T_a sensor were calibrated against a mercury thermometer. Flies with thermocouple implants were returned to the refrigerator until they were quiescent with T_{th} below the laboratory T_a (12.3–18.0°C), and were then placed on the laboratory bench under an opaque cup. When T_{th} approximated T_a the fly was uncovered and T_{th} and T_a were recorded at 2-s intervals by a microcomputer. Warm-up was often initiated upon removal of the cup, but some individuals required gentle prodding.

Thermal conductance

Freshly-killed syrphid flies were implanted with a thoracic thermocouple as above and heated to about 45°C using an incandescent lamp. Heated flies were quickly moved into a wind tunnel (wind speed = 5.6 m s⁻¹) and T_{th} and T_a were recorded at 5-s intervals by a microcomputer. In flies and bumblebees where the thorax was covered with pile, cooling rate was measured first with the pile intact and then again after the pile had been scraped from the thorax.

Data are presented as mean \pm standard deviation unless otherwise noted. Student's *t*-test (significance level = 0.05) was used to test differences between means and the significance of regressions.

RESULTS

Thoracic temperature

It is common practice to express thermoregulatory ability in terms of the slope of the regression of T_{th} on T_a . A slope not significantly different from zero indicates excellent thermoregulation, whereas a slope not significantly different from one indicates no thermoregulation. Clearly the accuracy of this test depends on how well the data set represents the thermal relationships of the insect. In some of the less common syrphid species we did not obtain significant regressions, presumably owing to small data sets and large amounts of scatter. For these species we give regression statistics but omit regression lines in Figs 1 and 2. For species where we obtained significant regressions the regression lines are included in those figures.

The syrphids we studied were active at T_a from at least 12.8 to 27.4°C and, over this range, the T_{th} of four *Bombus* mimics typically ranged from 25 to 35°C (Fig. 1). Thoracic temperature averaged 9.8–14.6°C above T_a depending on the species. In

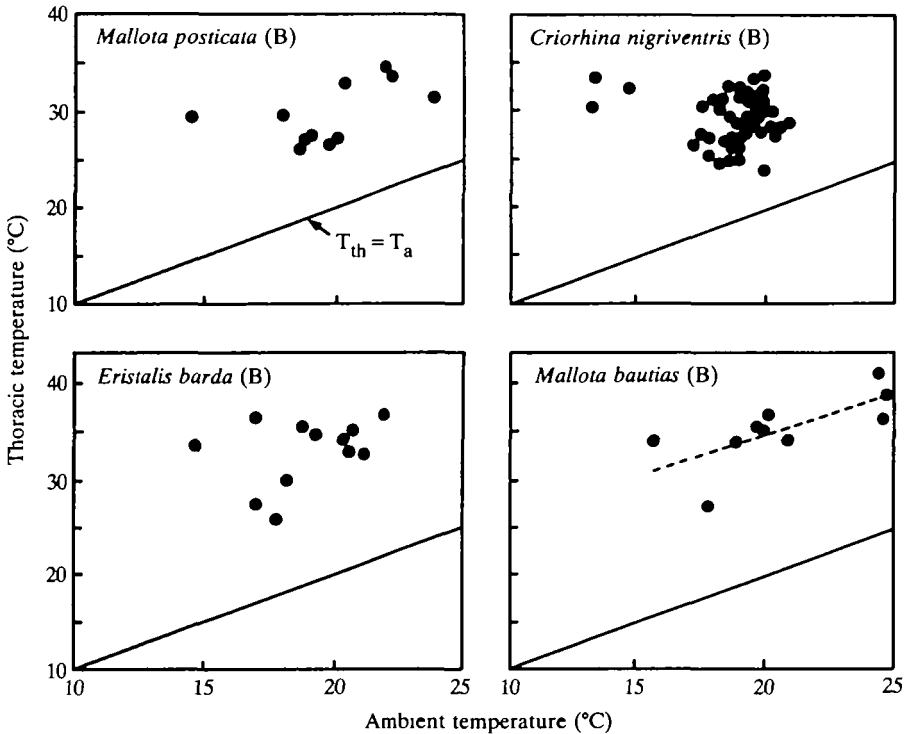


Fig. 1. The relationship of thoracic temperature to ambient temperature for four pubescent *Bombus* mimics (B). The solid line is the isotherm where points would lie if thoracic temperature and ambient temperature were equal.

three of the four species, regressions of T_{th} on T_a were not significant (*Mallota posticata*, $y = 22.1 + 0.57x$, $r^2 = 0.120$, $N = 12$, $P = 0.33$; *Criorhina nigriventris*, $y = 33.4 - 0.24x$, $r^2 = 0.012$, $N = 45$, $P = 0.36$; *Eristalis barda*, $y = 17.1 + 0.63x$, $r^2 = 0.260$, $N = 11$, $P = 0.16$). In *M. bautias*, however, a significant regression was obtained ($y = 17.5 + 0.86x$, $r^2 = 0.511$, $N = 10$, $P = 0.02$) and the slope of the regression relating T_{th} to T_a was not significantly different from 1 ($P = 0.65$), suggesting that T_{th} in this species is not actively regulated.

Thoracic temperatures of bumblebee queens and workers (*Bombus* spp.; presumptive models for the above four syrphids), taken concurrently and at the same locations where the syrphids were studied, averaged $17.9 \pm 3.02^\circ\text{C}$ above T_a (range = 11.6 – 26.5°C , $N = 72$). Body masses of the bumblebees averaged 0.293 ± 0.127 g (range = 0.050 – 0.695 g, $N = 68$).

Thoracic temperatures of four *Vespula*-mimicking syrphids, one *Dolichovespula*-mimic and two non-mimetic syrphids, all having little or no thoracic pile, were also elevated (Fig. 2). Thoracic temperatures of these flies averaged 9.9 – 12.8°C above T_a . The slopes of regressions relating T_{th} to T_a for *Temnostoma vespiforme* and *Sericomyia chrysotoxoides* ($y = 16.2 + 0.72x$, $r^2 = 0.389$, $N = 41$, $P < 0.001$ and $y = 6.5 + 1.18x$, $r^2 = 0.672$, $N = 17$, $P < 0.001$, respectively) did not differ significantly from 1 ($P = 0.06$ and $P = 0.41$, respectively) suggesting that T_{th} is not

regulated in these species. The regression of T_{th} on T_a was not significant for *Eristalis* sp. ($y = 18.2 + 0.617x$, $r^2 = 0.166$, $N = 17$, $P = 0.13$). In both *T. alternans* and *Chrysoxum* sp., however, the slopes of the regressions of T_{th} on T_a were significantly different from 1 ($y = 19.0 + 0.58x$, $r^2 = 0.199$, $N = 43$, $P = 0.03$ and $y = 24.7 + 0.31x$, $r^2 = 0.241$, $N = 32$, $P < 0.001$, respectively) suggesting that T_{th} is regulated in these species. Regressions were not performed on data for *Se. militaris* and *Se. lata* due to small sample sizes.

T_{th} of yellowjacket wasps (*Vespa vulgaris*; presumptive model for four of the above syrphids) taken concurrently and at the same locations where the syrphids

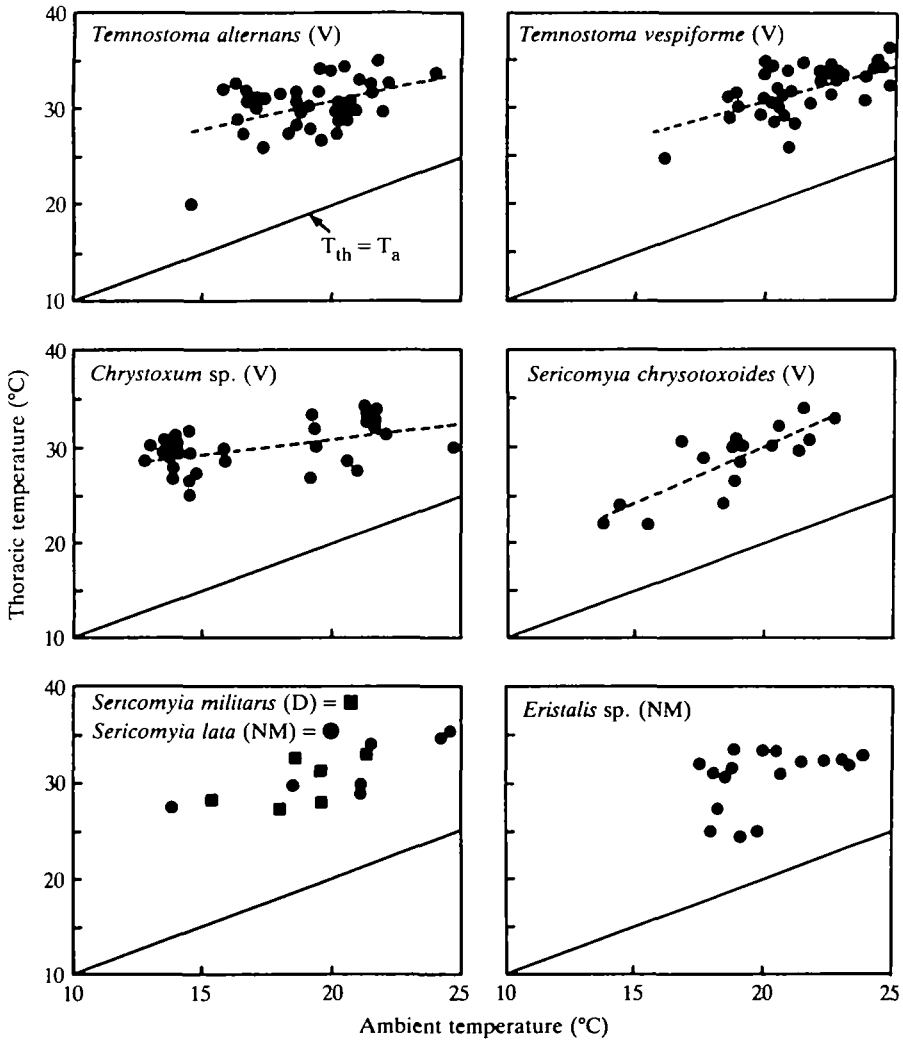


Fig. 2. The relationship of thoracic temperature to ambient temperature for six glabrous syrphids. (V) denotes *Vespa* mimics, (D) denotes *Dolichovespula* mimics and (NM) denotes non-mimetic species. The solid line is the isotherm where points would lie if thoracic temperature and ambient temperature were equal.

were studied averaged $15.5 \pm 5.48^\circ\text{C}$ above T_a (range = $6.5\text{--}27.5^\circ\text{C}$, $N = 13$). Body masses of the wasps averaged $0.154 \pm 0.052\text{ g}$ (range = $0.055\text{--}0.199\text{ g}$, $N = 13$). Thoracic temperatures of white-faced hornets (*Dolichovespula maculata*; presumptive model for one of the above syrphids) averaged $15.5 \pm 3.46^\circ\text{C}$ above T_a (range = $11\text{--}23.5^\circ\text{C}$, $N = 26$). Body masses of the hornets averaged $0.291 \pm 0.095\text{ g}$ (range = $0.144\text{--}0.463\text{ g}$, $N = 26$).

There were no significant differences in temperature excess ($T_{th} - T_a$) correlated with behaviour (e.g. foraging, basking, flight and patrolling, i.e. males searching for females) in the flies we studied. Likewise, there were no significant differences in the temperature excess between pubescent *Bombus* mimics and glabrous syrphids or between mimetic and non-mimetic syrphids.

Warm-up and sustained endothermy

Endothermic warm-up was signalled by the onset of periodic abdominal pumping movements. Most flies warmed spontaneously from $T_{th} = T_a$ ($12.3\text{--}18.0^\circ\text{C}$) after initially being gently prodded: warm-up rates ranged from $1.2\text{--}5.5^\circ\text{C min}^{-1}$, and were strongly dependent on body mass (Fig. 4; warm-up rates plotted in this figure were measured at T_a between 15 and 18°C). Some individuals increased T_{th} only a few degrees while others increased T_{th} to as high as 15°C above T_a (see, for example, Fig. 3). Warm-up usually ended with a flight attempt, followed by an immediate decline in T_{th} . The T_{th} at take-off ranged as follows: *Cr. nigriventris*, $21.2\text{--}27.3^\circ\text{C}$; *M. posticata*, $23.5\text{--}26.9^\circ\text{C}$; *T. alternans*, $18.7\text{--}24.1^\circ\text{C}$; *Se. lata*, 21.8°C ; *Sphecomyia vittata*, 20.4°C ; *T. vespiforme*, 23.8°C . In some syrphid species (*Cr. nigriventris*, *Se. lata*, *Sp. vittata*, *Chrysotoxum* sp.) warm-up was accompanied by an audible whining or buzzing; in others (*M. posticata*, *M. bautias*, *E. barda*, *T. alternans*, *T. vespiforme*) warm-up was silent. Heinrich & Pantle (1975) noted a correlation between wing movements and noise during warm-up in *Syrphus* sp. We sometimes noted minute wing movements during audible warm-ups, but the association between wing motion and noise was inconsistent. In any event, it is clear that in many species of syrphids warm-up can be independent of wing movements or noise.

Flies sometimes sustained endothermy beyond the 2–5 min necessary for T_{th} to reach flight temperature (Fig. 5). One 0.281-g *Cr. nigriventris* maintained an average $T_{th} - T_a$ difference of 13.4°C for more than 26 min (Fig. 5).

Thermal conductance

Thermal conductance of *Bombus* mimics (*Cr. nigriventris*, *M. posticata*, *M. bautias*, *E. barda*) and *Vespula* mimics (*T. alternans*, *T. vespiforme*) was highly dependent on body mass (Fig. 6), and conductance of *Bombus* mimics was on the average lower than that of similarly sized *Vespula* mimics (presumably reflecting the presence of insulating pile in *Bombus* mimics).

Removal of pile from the thorax of *Bombus* mimics and *Bombus* spp. significantly increased thermal conductance (Fig. 7, $P < 0.01$ for all cases). Thermal conductance of *Cr. nigriventris* increased by an average of 32% after the pile had been removed.

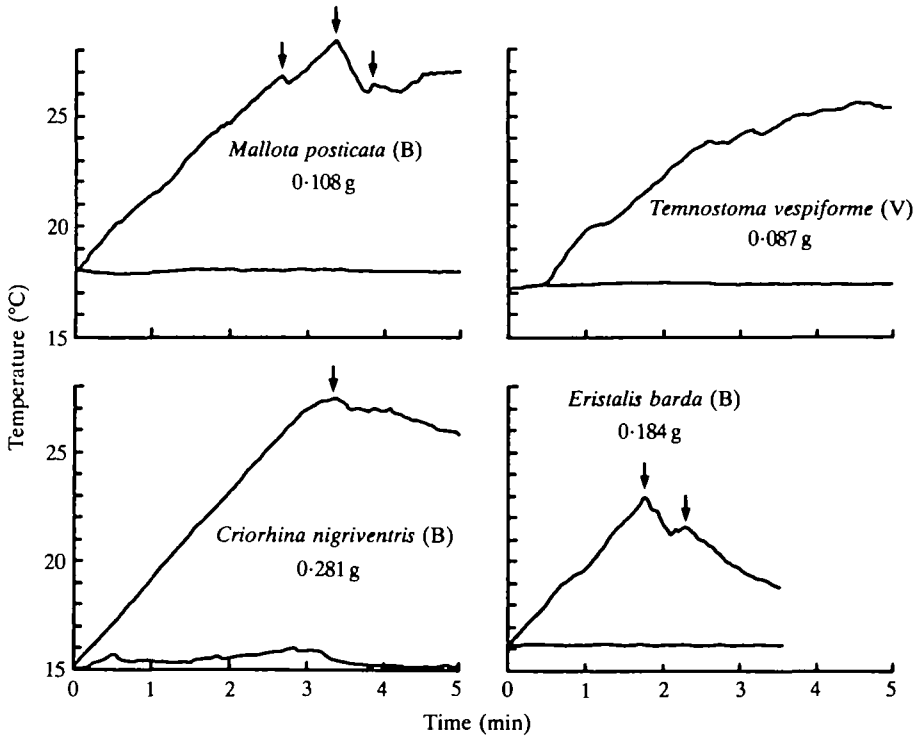


Fig. 3. The relationship of thoracic temperature to time taken for endothermic warm-up in four species of syrphid flies. (B) denotes *Bombus* mimics and (V) denotes *Vespula* mimics. The upper solid line represents thoracic temperature; the lower solid line represents ambient temperature. The arrows indicate flight attempts.

Thermal conductances of the other three *Bombus* mimics are combined in Fig. 7 because all have similar short, stiff hairs whereas *Cr. nigriventris* has relatively long hairs. The removal of pile increased thermal conductance of these other *Bombus* mimics by an average of 30%. Thermal conductance of *Bombus* queens and workers increased by 25% under the same conditions after removal of the thoracic pile.

DISCUSSION

Thermoregulation in flies is of considerable interest because their small size renders them subject to rapid rates of heat exchange while their flight muscles presumably require a high temperature to support their typically high flight speeds. Behavioural thermoregulation tends to be quite important in small, diurnal species. For example, Arctic mosquitoes (*Aedes* spp.) bask in the parabolic corollas of flowers that provide no nectar (Hocking & Sharplin, 1965). Light-seeking neotropical robber flies and desert robber flies regulate their high body temperatures while foraging largely by microhabitat selection and postural adjustments (Morgan, Shelly & Kimsey, 1985; K. R. Morgan & T. E. Shelly, in preparation).

■ Most previous studies of insect endothermy have focused on large moths, bees and beetles. Many dipterans are so small that dependence on metabolically generated

heat for thermoregulation has been considered unlikely. In the blowfly (*Calliphora*), a temperature increase due to endothermy of only 0.75°C has been measured (Digby, 1955), and thoracic temperature of the sheep blowfly (*Phaenicia*) remains within 1.5°C of T_a during tethered flight (Yurkiewicz & Smyth, 1966). Nevertheless, some relatively small syrphids ($<0.03\text{ g}$) maintain a high T_{th} by a combination of shivering and basking while they congregate at leks (Heinrich & Pantle, 1975; Gilbert, 1984), woodland tabanid and pantophthalmid flies ($0.9\text{--}2.8\text{ g}$) warm endothermically before flight (May, 1976; Bartholomew & Lighton, 1986), and the horse bot-fly (*Gasterophilus*; $0.03\text{--}0.24\text{ g}$) elevates T_{th} by as much as 12°C in preparation for flight, and it maintains T_{th} at variable high levels during tethered flight (Humphreys & Reynolds, 1980).

Thoracic temperature

With the exception of *Crysotoxum* sp., the lekking behaviour observed in *Syrphus* spp. (Heinrich & Pantle, 1975; Gilbert, 1984) is absent in the flies we studied. High T_{th} is therefore not a special adaptation of lekking syrphids.

High T_{th} is essential for normal activity in the syrphids we studied. It seems that, rather than being a special adaptation for mimicry, the primary importance of high T_{th} is to permit normal foraging and/or mate searching at low T_a . Non-mimetic syrphids that we studied (*Se. lata* and *Eristalis* sp.) maintain T_{th} at equally high levels during activity. A variety of other non-mimetic Diptera maintain T_{th} at similar levels during activity, including tachinids (Chappell & Morgan, 1987) and calliphorids and bombyliids (B. Heinrich & K. R. Morgan, unpublished data).

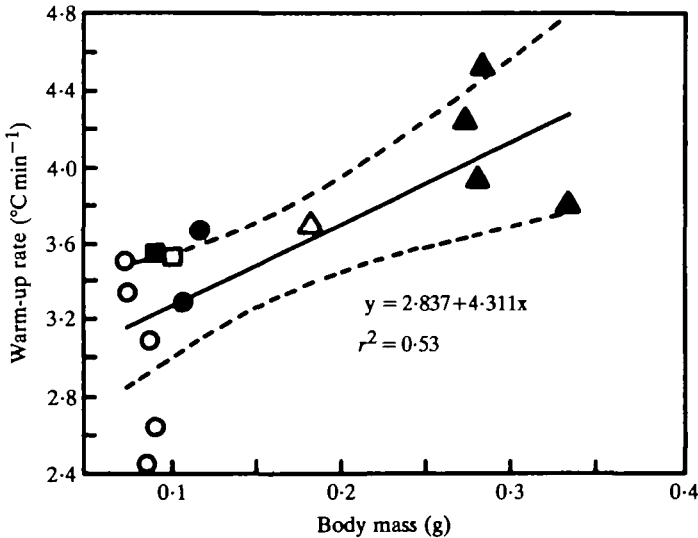


Fig. 4. The relationship of warm-up rate to body mass for various syrphids at ambient temperatures between 15 and 18°C . \circ , *Temnostoma alternans*; \bullet , *Mallota posticata*; \square , *Sericomyia slossonae*; \blacksquare , *Sericomyia lata*; \triangle , *Eristalis barda*; \blacktriangle , *Criorhina nigriventris*. The solid line represents the least squares regression of warm-up rate on mass. The dashed lines are the 95% confidence intervals for the regression.

However, high T_{th} may have been an important preadaptation for the evolution of mimicry in syrphid flies. In addition to physical characteristics of syrphids which are overtly mimetic, much of their inflight behaviour, including the flight tone (Brower & Brower, 1965), closely resembles that of the model. In fact, the mimicry of many of the flies we studied appeared to be most accurate during flight. If high T_{th} increases flight speed and manoeuvrability in flying insects (see, for example, Heinrich, 1979, 1983; Morgan *et al.* 1985) it may also be important in allowing syrphids to copy the flight behaviour of their highly endothermic models.

Thermoregulation during activity in the syrphids we studied was less effective than in their hymenopteran models, as indicated by comparisons of temperature excess and the degree of independence of T_{th} and T_a (i.e. the slopes of regression lines relating T_{th} to T_a). The temperature excesses of bumblebee mimics averaged 3.3–8.1°C below those of *Bombus*, while those of wasp mimics averaged 2.7–5.6°C below those of *Vespula* and *Dolichovespula*, their models. Only in *T. alternans* and *Chrysotoxum* sp. did the regressions of T_{th} on T_a have slopes significantly different

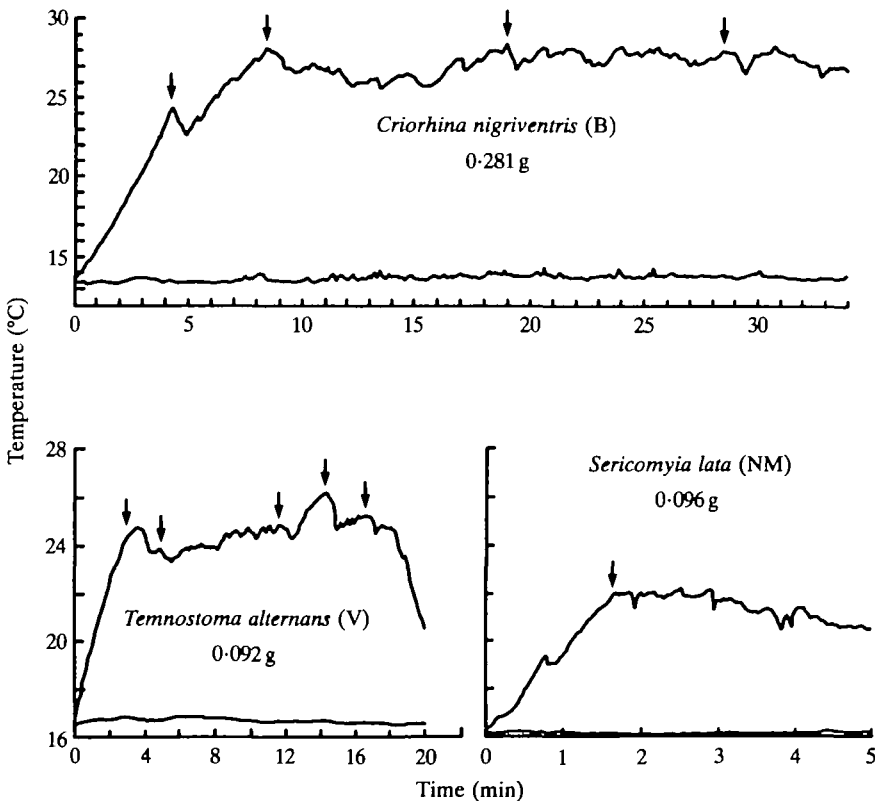


Fig. 5. The relationship of thoracic temperature to time taken for endothermic warm-up and sustained endothermy in three species of syrphid flies. (B) denotes *Bombus* mimics, (V) denotes *Vespula* mimics and (NM) denotes non-mimetic species. The upper solid line represents thoracic temperature; the lower solid line represents ambient temperature. The arrows represent flight attempts.

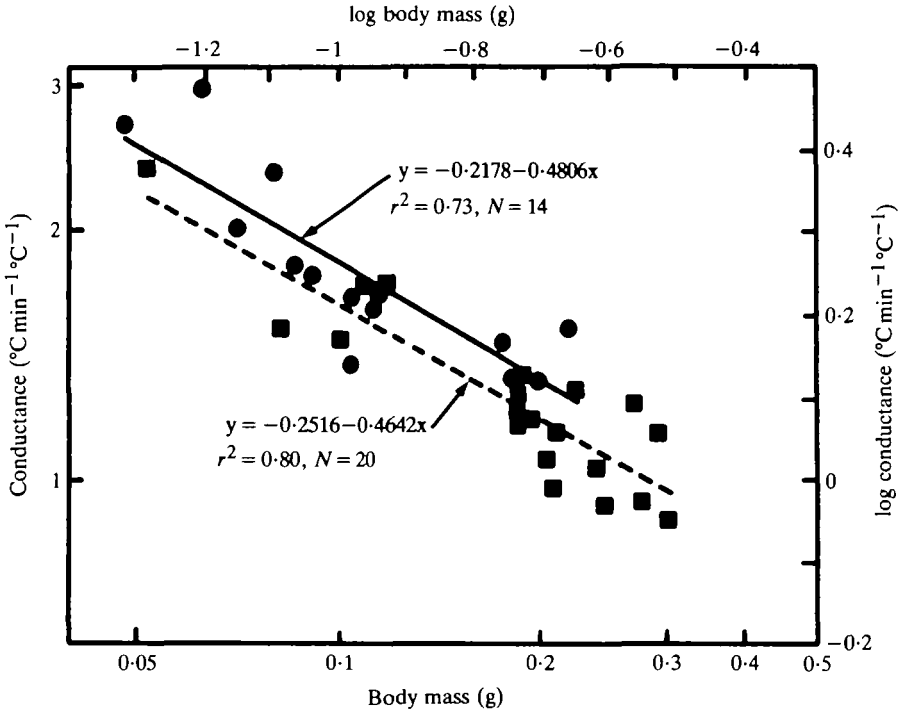


Fig. 6. The relationship of thermal conductance to body mass for *Bombus* mimics (solid squares) with pile intact and *Vespula* mimics (solid circles) at a wind speed of 5.6 m s^{-1} . The solid line and dashed line represent least squares regressions of log conductance on log body mass for *Vespula* mimics and *Bombus* mimics, respectively.

from 1 (0.58 and 0.31 , respectively), indicating some regulation of T_{th} . This partial regulation of T_{th} is similar to the levels of thermoregulation seen in *Syrphus* sp. (Heinrich & Pantle, 1975) and *Syrphus ribesii* (Gilbert, 1984). In contrast, *Bombus* queens and workers achieve almost perfect regulation of T_{th} (slopes not significantly different from 0) at T_a between 2.5 and 25°C (Heinrich & Heinrich, 1983). Likewise, *Vespula* and *Dolichovespula* achieve excellent regulation of T_{th} at T_a between 5 and 21°C and between 2 and 23°C , respectively (Heinrich, 1983).

There was no apparent relationship between body mass and temperature excess in the syrphid flies we studied ($P = 0.59$). Likewise, body mass and temperature excess were not significantly related in the bumblebees, yellow-jacket wasps or white-faced hornets ($P = 0.22$, $P = 0.49$ and $P = 0.25$, respectively). The mean body masses of *Bombus*-mimicking species ranged from 0.115 to 0.207 g, whereas the mean mass of the bumblebees we studied was 0.293 g. Mean body masses of *Vespula* and *Dolichovespula* mimics ranged from 0.067 to 0.134 g, whereas mean masses of the wasps and hornets were 0.154 and 0.291 g, respectively. Differences in thermoregulatory ability between the flies and their models may result in part from increased rates of heat loss due to the smaller body sizes of the flies although, where the body masses of mimics and models overlapped, the differences in temperature excess were still apparent.

Endothermic warm-up and sustained endothermy

In general, small heterotherms warm up more rapidly than large ones, but previous data relating the rate of endothermic warm-up to body mass in insects have shown either no relationship (Heinrich & Bartholomew, 1971; Heinrich & Casey, 1973; Bartholomew & Epting, 1975) or a weak positive correlation (May, 1976). Our data for maximum rate of warm-up in syrphid flies show a strong positive correlation with body mass (Fig. 4); in contrast to vertebrate heterotherms, small syrphids warm up more slowly than large syrphids.

The capacity for sustained endothermy has been demonstrated in a variety of bees and beetles but only once previously (to a very limited extent) in a fly. In the laboratory, the giant tropical fly (*Pantophthalmus tabaninus*) alternates between rest and sustained endothermy where T_{th} remains 1–2°C above T_a , sometimes for more than 30 min (Bartholomew & Lighton, 1986). The capacity for sustained endothermy is much more highly developed in syrphids. Three of the syrphid species we studied showed pronounced tendencies to maintain T_{th} at high and fairly constant levels (Fig. 5). It seems likely to us that further testing would demonstrate that the response is common in larger syrphids because we at no time observed torpid flies during our extensive observations of foraging flies in the field. The syrphids did not show a clear pattern of periodic cycling of T_{th} during sustained endothermy in the laboratory, such as that seen in beetles (Morgan & Bartholomew, 1982; Morgan, 1987). However, frequent attempts at flight by the flies may have obscured the cycles.

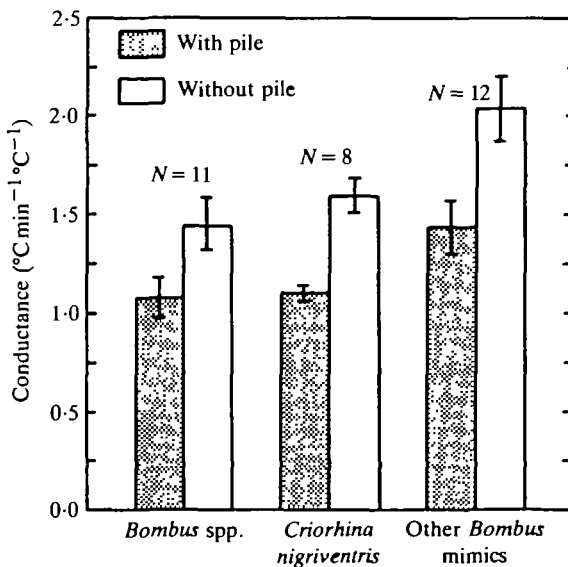


Fig. 7. Thermal conductance measured at a wind speed of 5.6 ms⁻¹ before and after removal of the thoracic pile for *Bombus* spp. and *Bombus* mimics. The category 'other *Bombus* mimics' includes *Mallota posticata*, *M. bautias* and *Eristalis barda* which have very similar short, dense pile. *Criorhina nigriventris* has longer pile. The confidence intervals shown represent $\pm 2S.E.$ of the mean.

Sustained endothermy may allow the flies to maintain a state of flight readiness during foraging that would not be possible if T_{th} were allowed to fall to T_a . A continuously high T_{th} may also enhance predator avoidance and may enable the flies to assimilate nutrients more rapidly during foraging and/or enhance growth rates of reproductive cells. The high energetic cost of sustained endothermy may be relatively unimportant even in small flies if there is always a ready source of nectar to fuel their endothermy. Unlike social bees, the flies need not expend energy supplies for nest thermoregulation, and they do not store energy supplies for their relatives and/or offspring.

Thermal conductance

Although the thick pile of *Bombus* mimics is clearly effective as insulation, the cooling rates and body temperature excesses of these mimics are similar to those of glabrous syrphids. This suggests that the pubescence characteristic of *Bombus* mimics did not evolve solely as insulation. Unlike bumblebees and honeybees, which obtain much of their pollen during foraging by combing it from their hairs, syrphids are primarily direct feeders (Gilbert, 1981). If this is true for the *Bombus* mimics we studied, it is unlikely that their pubescence evolved in response to pollen-gathering behaviour, as suggested for *Eristalis tenax* by Holloway (1976). It seems most likely that the primary importance of pubescence in *Bombus* mimics is in improving visual mimicry, and that its importance in insulating the thorax is secondary.

We are indebted to C. H. Morgan for much technical assistance, G. S. Waldbauer for identifying the flies, and J. R. B. Lighton for the use of programs for the BBC microcomputer. We also thank M. A. Chappell and an anonymous reviewer for critically reading the manuscript. This study was funded in part by an intramural grant from the University of Vermont.

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