

RELATIONSHIP OF WING BEAT FREQUENCY AND TEMPERATURE DURING TAKE-OFF FLIGHT IN TEMPERATE-ZONE BEETLES

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Accepted 16 May 1989

Summary

In 24 species of temperate-zone beetles thoracic temperatures (T_{th}), and wing beat frequency (n) were measured over a range of ambient temperatures (T_a) during take-off flight. The sensitivity of wing beat frequency to thoracic temperature varied greatly in different species: Q_{10} values ranged from 0.8 to 1.3. The wing beat frequency of beetles with higher average n was more sensitive to thoracic temperature. It is suggested that the temperature sensitivity of wing beat frequency results from temperature-dependent changes in the resonant properties of the beetle flight system rather than from changes in the temperature sensitivity of the muscle or nervous system.

There was large variability in thermoregulatory precision. Beetles with higher n tended to thermoregulate more precisely than beetles with lower n . Measurements of thoracic temperature before and after flight indicated endothermic heat production during pre-flight activity, but not during the brief take-off flights.

Introduction

Wing beat frequency is one of the major components of the aerodynamic system of flying insects, strongly affecting lift production and, therefore, closely tied to the energetic requirements during flight (Casey, 1989). Consequently, numerous authors have studied various factors influencing wing beat frequency (Sotavalta, 1947; Greenewalt, 1962; Weis-Fogh, 1973, 1977; Lighthill, 1977; Casey & May, 1982; Ellington, 1984). Because temperature is an important factor determining energy metabolism, several authors have specifically studied the effect of temperature on wing beat frequency. Sotavalta (1947) was among the first authors to observe temperature-induced changes in wing beat frequency, and further studies are summarized by May (1981): temperature sensitivity of n varied greatly in different taxa, although increases in wing beat frequency were generally coupled with increases in thoracic temperature, with Q_{10} values in the range 1.0–1.4.

Because different wing beat frequencies may be coupled to differences in energy

Key words: Coleoptera, wing beat frequency, thermoregulation.

metabolism, and because energetic differences in turn affect heat production, wing beat frequency may have an effect on thermoregulation. Numerous insects show a capacity for thermoregulation (May, 1985; Casey, 1988). In beetles, endogenously elevated temperatures, a prerequisite for non-behavioural thermoregulation, were first observed by Krogh & Zeuthen (1941) in *Geotrupes stercorarius*. Bartholomew & Casey (1977a,b) reported elevated body temperatures during terrestrial locomotion in tropical beetles, and African dung beetles were observed to maintain high body temperatures while making and rolling dung balls (Bartholomew & Heinrich, 1978; Heinrich & Bartholomew, 1979). Further indications for endothermy were found in the elephant beetle *Megasoma elephas* (Morgan & Bartholomew, 1982) and in the green fig beetle *Cotinus texana* (Chappell, 1984). A flower scarab *Pachynotus sinuata*, in contrast, was observed to warm up only prior to flight while maintaining body temperatures near ambient during foraging (Heinrich & McClain, 1986). Finally, Morgan (1987) was able to show a thoracic temperature excess of 35°C in Californian rain beetles *Plecoma* spp. The above studies, however, did not include measurements of wing beat frequency and, consequently, the present study is the first, to my knowledge, to relate the two factors in beetles.

This study considers take-off flight. During take-off a beetle must accelerate and equilibrate, and therefore energy requirements should be higher than during regular flight. In both *Popillia japonica* and *Chauliognathus pennsylvanicus* rates of oxygen consumption were significantly higher during take-off flight than in continuous flight (J. J. Oertli & M. Oertli, in preparation). Because take-off flight is energetically more demanding, it should also be more limiting than normal flight.

Materials and methods

Twenty-four species of beetles representing 10 families (see Table 1) were considered in the present study. With the exception of *Oulema melanopus* and *Chauliognathus marginatus* all beetles were measured in the vicinity of New Brunswick, NJ, USA. *O. melanopus* was collected south of Bern, Switzerland, and *C. marginatus* was measured in southern Florida, USA. Field measurements were made during 1987 and 1988.

Wing beat frequencies were measured with an optical tachometer (Unwin & Ellington, 1979), recorded on tape and determined on a storage oscilloscope. Because of the difficulty of observing beetles during free flight under field conditions, the following procedure was used: beetles were captured with a net or light trap and subsequently placed in a small box (0.5 dl), open at the top, which in turn was placed in a larger, transparent 20 l plastic container. In most cases the beetles climbed to the top of the smaller box and then took off. During this period of free flight, wing beat frequencies were measured. Immediately upon landing on the rim of the larger container, the beetles were captured and their thoracic temperature measured by placing a 0.1 mm diameter copper-constantan thermo-

couple contained in a hypodermic needle into their thorax. The measurement of thoracic temperature occurred within 1–2 s after the beetle landed on the rim of the larger container. Temperatures were recorded with a Sensortek BAT-12 or Cole Parmer Digi-Sense thermocouple thermometer. All trials were undertaken in a shaded environment to prevent radiative heat gain. Simultaneous measurements of ambient shade temperature were taken immediately after thoracic temperature had been measured. All beetles were measured within 15 min of capture. Beetles were kept in a shaded environment during the time from capture to testing and were not allowed to fly during this period.

To have an indication of the size of the thoracic temperature change during the period of flight considered, thoracic temperatures in five species (see Table 4) were measured in 15 individuals per species immediately before placing the beetles in the small container described above and immediately after a take-off flight lasting 1–2 s. Although ambient temperature was different among species, it remained constant in all individuals of a given species.

Subsequent to field measurements, beetles were taken to the laboratory, where they were killed by freezing, prior to determining body mass to the nearest milligram.

Results

Temperature sensitivity of wing beat frequency

Outlines of 12 representative species are pictured in Fig. 1. Average body masses ranged from 3.3 to 206 mg and average wing beat frequencies ranged from 60.9 to 118.5 Hz (Table 1). Body mass was negatively correlated with wing beat frequency (Spearman rank correlation coefficient -0.517 , $P = 0.01$; Fig. 2). This result corresponds to the situation in other insect orders and for flying animals in general (Greenewalt, 1962). A detailed interspecific analysis of the scaling of wing beat frequency with morphology in beetles will be presented elsewhere (J. J. Oertli, in preparation).

Thoracic temperature (T_{th}) had a strongly variable influence on wing beat frequency (n) as a function of the species considered. Fig. 3 shows the raw data demonstrating the effects of thoracic temperature on wing beat frequency for two species of beetles. Regression equations for all 24 species are given in Table 2. Q_{10} values are used to describe the effects of temperature on n , because this index allows comparison of widely varying frequencies. Although Q_{10} values are generally used to describe processes exponentially dependent on temperature, this index can be used to describe linear relationships if specific temperature intervals are given.

Considerable effects of T_{th} on n were observed in *Agriotes* sp., *Oulema melanopus*, *Popillia japonica* and *Chauliognathus pennsylvanicus* (Q_{10} in the region of 1.2–1.3), whereas n only increased slightly over a range of T_{th} in most other species (Q_{10} in the region of 1.1). In several species (e.g. *Coccinella*

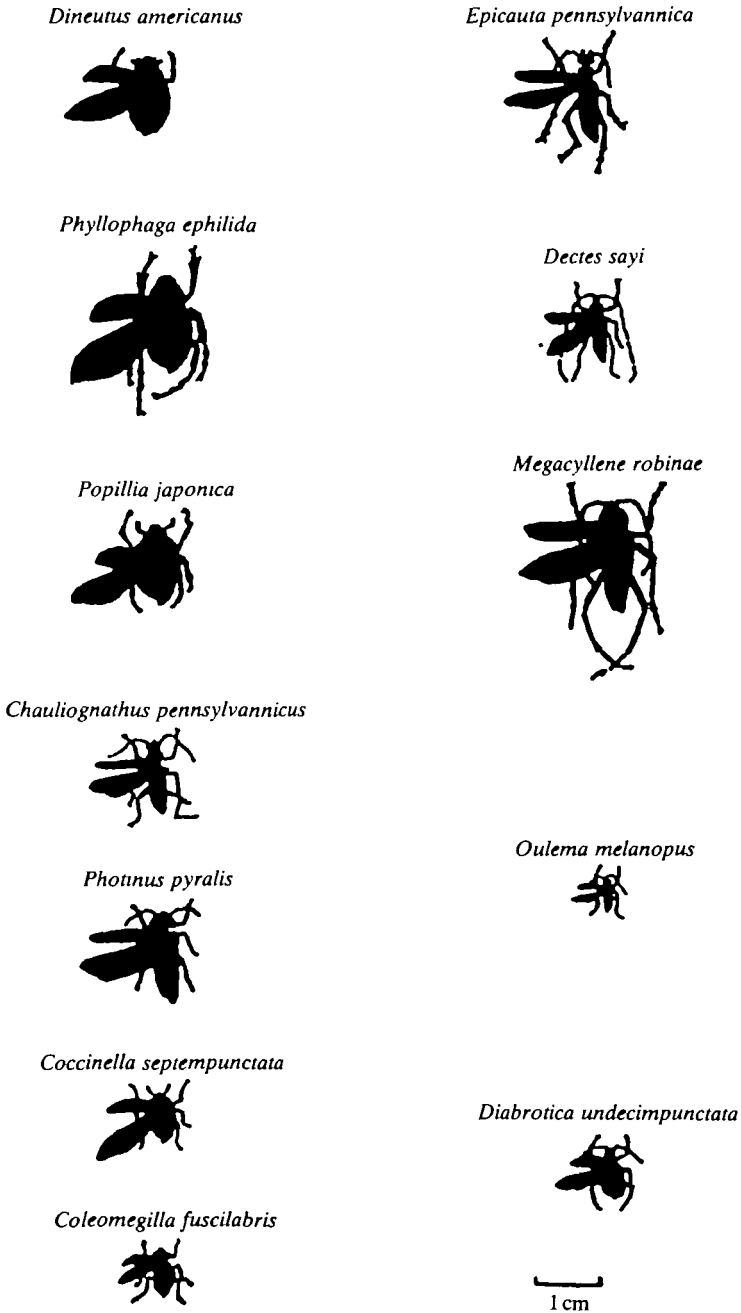


Fig. 1. Outlines of 12 representative species of beetles used in the study.

septempunctata, *Phyllophaga ephilida*) no effects of T_{th} on n were found (a Q_{10} of 1.0). Finally, in some species (e.g. *Dineutus americanus*) wing beat frequencies decreased with increases in thoracic temperature ($Q_{10} < 1.0$). Both linear and

Table 1. Averages and standard deviations of wing beat frequency and body mass

Species	Ref. no.	N	Wing beat frequency (Hz)	Body mass (mg)
Gyrinidae				
<i>Dineutus americanus</i> Fabricius	1	29	73.8 ± 16.10	49.16 ± 7.34
Scarabaeidae				
<i>Diplotaxis frondicola</i> Say	2	50	78.9 ± 5.16	23.80 ± 6.47
<i>Hoplia limbata</i> LeConte	3	20	80.8 ± 10.70	56.70 ± 9.40
<i>Phyllophaga ephilida</i> Say	4	25	61.6 ± 6.30	205.89 ± 95.91
<i>Popillia japonica</i> Newman	5	100	118.5 ± 8.91	93.20 ± 19.99
Elateridae				
<i>Ctenicera</i> sp. Latreille	6	10	89.9 ± 9.31	28.40 ± 12.04
<i>Agriotes</i> sp. Eschscholtz	7	17	109.1 ± 14.30	11.90 ± 6.87
Cantharidae				
<i>Chauliognathus pennsylvanicus</i> DeGeer	8	102	88.7 ± 5.80	38.49 ± 15.01
<i>Chauliognathus marginatus</i> Fabricius	9	12	86.7 ± 7.31	21.08 ± 9.01
<i>Cantharis bilineatus</i> Say	10	25	89.8 ± 7.95	16.68 ± 7.59
Lampyridae				
<i>Lucidota atra</i> Fabricius	11	22	64.7 ± 7.60	42.50 ± 19.67
<i>Photinus pyralis</i> Linné	12	75	60.9 ± 4.90	25.91 ± 8.96
Coccinellidae				
<i>Coccinella septempunctata</i> Linné	13	30	76.9 ± 9.10	30.60 ± 11.55
<i>Coleomegilla fuscilabris</i> Mulsant	14	61	95.2 ± 10.81	12.14 ± 2.96
<i>Cycloneda sanguinea</i> Linné	15	21	96.1 ± 10.21	9.80 ± 3.30
<i>Hippodamia convergens</i> Guérin	16	35	78.0 ± 9.90	13.00 ± 4.51
Meloidae				
<i>Epicauta pennsylvanica</i> DeGeer	17	51	88.1 ± 6.93	55.23 ± 19.47
Cerambycidae				
<i>Pidonia ruficollis</i> Say	18	21	93.3 ± 6.22	6.03 ± 2.71
<i>Dectes sayi</i> Dillon & Dillon	19	57	92.0 ± 8.21	13.59 ± 4.86
<i>Megacyllene robiniae</i> Forster	20	35	89.0 ± 10.36	116.40 ± 63.68
Chrysomelidae				
<i>Diabrotica longicornis</i> Say	21	42	100.9 ± 7.20	7.05 ± 2.97
<i>Diabrotica undecimpunctata</i> Barber	22	47	84.9 ± 8.90	18.33 ± 5.90
<i>Oulema melanopus</i> Linné	23	49	117.0 ± 11.8	3.33 ± 1.05
Curculionidae				
<i>Lixus concavus</i> Say	24	12	101.9 ± 31.39	20.33 ± 6.11

exponential models fit the data equally well: regressions of either n or $\log n$ on T_{th} gave approximately equal correlation coefficients (e.g. *Popillia japonica*: $r = 0.480, 0.471$; *Epicauta pennsylvanica*: $r = 0.309, 0.312$; *Chauliognathus penn-*

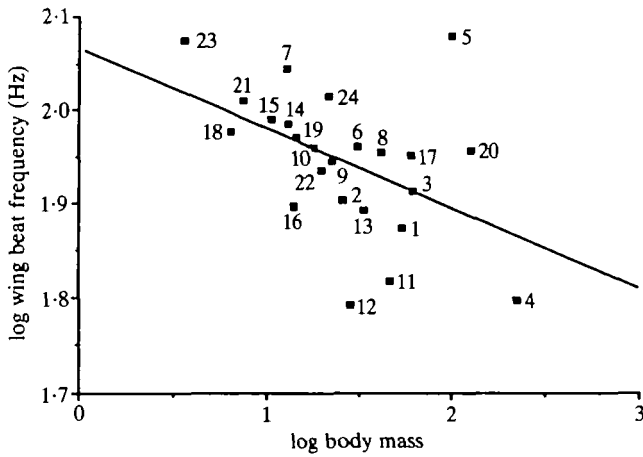


Fig. 2. Relationship between mean wing beat frequency (Hz) and body mass (mg). Numbers adjacent to data points in this and later figures correspond to the species reference number given in Table 1. Linear regression equation: $y = 2.057 - 0.085x$, $r = 0.469$, $P < 0.05$.

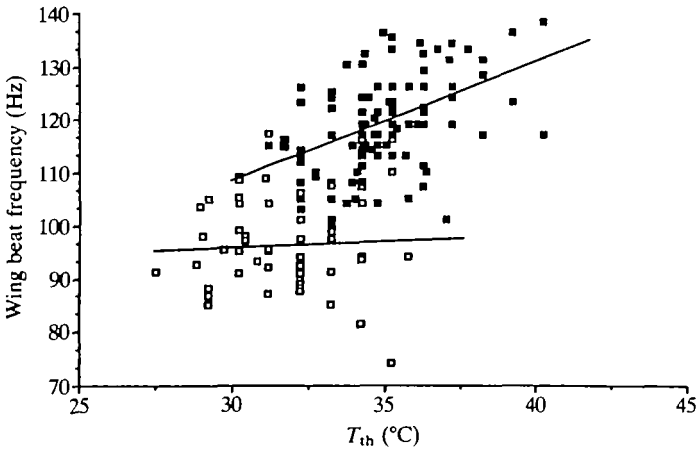


Fig. 3. Wing beat frequencies over a range of thoracic temperatures (T_{th}) for *Coleomegilla fuscilabris* (\square) (linear regression equation: $y = 39.97 + 2.26x$, $r = 0.480$, $P < 0.05$) and *Popillia japonica* (\blacksquare) (linear regression equation: $y = 89.73 + 0.17x$, $r = 0.030$, not significant, $P > 0.05$).

sylvanicus: $r = 0.458$, 0.546 for linear vs logarithmic models, respectively). Therefore, for reasons of convenience, a linear model is used.

In Fig. 4, the Q_{10} of the regression line of thoracic temperature sensitivity is plotted against the average wing beat frequency of a species (in this graph, as in all subsequent figures, Q_{10} is taken at face value, even if the regression did not produce significant correlations between n and T_{th}). Beetles with higher average

Table 2. Linear regression equations, standard errors and Q_{10} values of thoracic temperature sensitivity of wing beat frequency

Species	Ref. no.	N	Correlation coefficient	Slope	y-intercept	Range of T_{th} measured (°C)	Q_{10} (25–35°C)
Gyrinidae							
<i>Dineutus americanus</i>	1	29	0.30	-1.81 ± 1.76	136.25 ± 8.88	28–32	0.80
Scarabaeidae							
<i>Diplotaxis frondicola</i>	2	50	0.16	0.28 ± 0.31	71.05 ± 8.37	22–31	1.04
<i>Hoplia limbata</i>	3	20	0.33	0.70 ± 0.52	64.37 ± 13.71	23–32	1.09
<i>Phyllophaga ephialda</i>	4	25	0.12	-0.19 ± 0.51	67.68 ± 6.84	24–36	0.97
<i>Popillia japonica</i>	5	100	0.48	2.26 ± 0.42	39.97 ± 14.53	31–38	1.24
Elateridae							
<i>Ctenicera</i> sp.	6	10	0.48	1.66 ± 0.97	51.21 ± 22.94	26–33	1.17
<i>Agriotes</i> sp.	7	17	0.52	2.91 ± 1.23	15.56 ± 39.20	27–36	1.33
Cantharidae							
<i>Chauliognathus pennsylvanicus</i>	8	102	0.46	0.64 ± 0.12	69.65 ± 3.66	22–38	1.23
<i>Chaultognathus marginatus</i>	9	12	0.26	0.41 ± 0.49	74.16 ± 15.13	21–30	1.06
<i>Cantharis bilineatus</i>	10	25	0.42	1.02 ± 0.47	60.34 ± 13.71	24–32	1.11
Lampyridae							
<i>Lucidota atra</i>	11	22	0.21	-0.28 ± 0.30	73.38 ± 8.88	17–26	0.96
<i>Photinus pyralis</i>	12	75	0.31	0.54 ± 0.19	46.39 ± 46.39	22–38	1.09
Coccinellidae							
<i>Coccinella septempunctata</i>	13	30	0.09	-0.22 ± 0.48	83.81 ± 83.81	22–35	0.97
<i>Coleomegilla fuscilabris</i>	14	61	0.03	0.17 ± 0.17	89.73 ± 89.73	26–36	1.02
<i>Cycloneda sanguinea</i>	15	21	0.20	0.73 ± 0.86	73.74 ± 26.17	22–35	1.10
<i>Hippodamia convergens</i>	16	35	0.14	0.28 ± 0.36	69.89 ± 10.54	22–32	1.04
Meloidae							
<i>Epicauta pennsylvanica</i>	17	51	0.31	0.55 ± 0.24	69.25 ± 69.25	29–40	1.07
Cerambycidae							
<i>Pidonia ruficollis</i>	18	21	0.14	0.75 ± 1.25	69.23 ± 40.07	29–33	1.09
<i>Dectes sayi</i>	19	57	0.09	0.33 ± 0.49	81.00 ± 81.00	25–36	1.04
<i>Megacyllene robiniae</i>	20	35	0.52	1.62 ± 0.27	42.01 ± 42.01	20–39	1.20
Chrysomelidae							
<i>Diabrotica longicornis</i>	21	42	0.11	0.56 ± 0.88	84.19 ± 84.19	25–35	1.06
<i>Diabrotica undecimpunctata</i>	22	47	0.17	0.60 ± 0.60	66.04 ± 9.00	25–34	1.07
<i>Oulema melanopus</i>	23	49	0.51	3.21 ± 0.79	25.05 ± 10.67	25–33	1.31
Curculionidae							
<i>Lixus concavus</i>	24	12	0.697	1.455 ± 0.47	60.18 ± 0.47	31–40	1.15

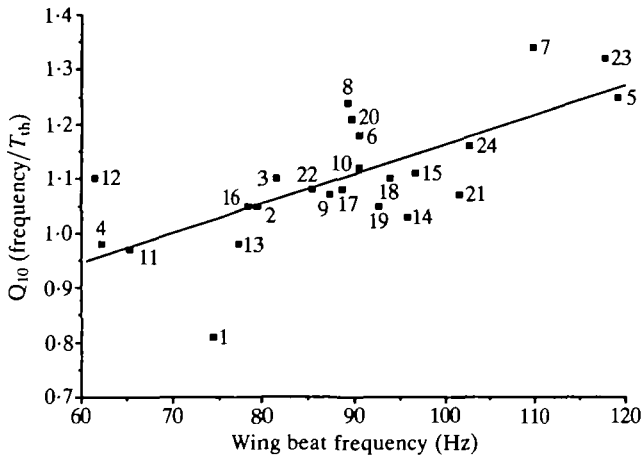


Fig. 4. Q_{10} values of thoracic temperature sensitivity of wing beat frequency plotted against average wing beat frequency. Q_{10} values were obtained from Table 2. Spearman rank correlation coefficient 0.661, $P < 0.0001$.

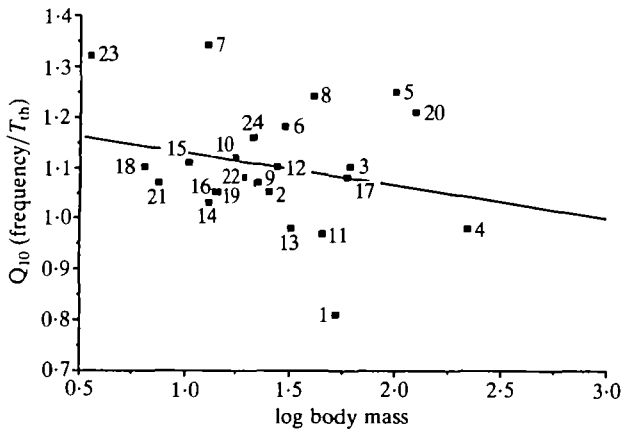


Fig. 5. Q_{10} values of thoracic temperature sensitivity of wing beat frequency plotted against average body mass (in mg). Spearman rank correlation coefficient -0.156 , not significant, $P > 0.05$.

wing beat frequencies displayed higher temperature sensitivity of frequency. In contrast, average body mass had no significant influence on the temperature sensitivity of wing beat frequency (Fig. 5).

As was the case for thoracic temperature, ambient temperature differentially influenced wing beat frequency (Table 3), although the observed differences were not as large as the ones observed for thoracic temperatures. Additionally, no correlation between ambient temperature sensitivity of wing beat frequency and average wing beat frequency or average mass was observed.

Table 3. Linear regression equations, standard errors and Q_{10} values of ambient temperature sensitivity of wing beat frequency

Species	Ref. no.	N	Correlation coefficient	Slope	y-intercept	Range of T_a measured (°C)	Q_{10} (25-35°C)
Gyrinidae							
<i>Dineutus americanus</i>	1	29	0.10	-0.09 ± 0.24	74.20 ± 2.65	25-36	0.99
Scarabaeidae							
<i>Diplotaxis fronticola</i>	2	50	0.16	0.24 ± 0.31	71.05 ± 8.37	20-29	1.03
<i>Hoplia limbata</i>	3	20	(T_a not measured)				
<i>Phyllophaga ephitida</i>	4	25	0.10	-0.14 ± 0.48	65.28 ± 6.86	18-31	0.98
<i>Popillia japonica</i>	5	100	0.01	0.10 ± 0.58	113.93 ± 17.76	24-36	1.01
Elatridae							
<i>Ctenicera</i> sp.	6	10	0.03	-0.11 ± 1.10	93.23 ± 32.90	19-29	0.99
<i>Agriotes</i> sp.	7	17	0.28	1.10 ± 1.02	76.56 ± 27.88	21-33	1.11
Cantharidae							
<i>Chauliognathus pennsylvanicus</i>	8	102	0.45	0.55 ± 0.11	73.57 ± 2.98	19-38	1.06
<i>Chauliognathus marginatus</i>	9	12	0.06	0.45 ± 0.76	74.16 ± 20.58	21-30	1.05
<i>Cantharis bilineatus</i>	10	25	0.31	0.58 ± 0.36	76.40 ± 8.614	16-28	1.06
Lampyridae							
<i>Lucidota atra</i>	11	22	0.12	0.20 ± 0.60	61.08 ± 13.15	17-26	1.03
<i>Photinus pyralis</i>	12	75	0.38	0.72 ± 0.21	43.54 ± 5.05	19-36	1.12
Coccinellidae							
<i>Coccinella septempunctata</i>	13	30	0.03	-0.12 ± 0.37	80.08 ± 9.38	17-34	0.98
<i>Coleomegilla fuscilabris</i>	14	61	0.22	0.19 ± 0.53	89.49 ± 15.78	23-35	1.02
<i>Cycloneda sanguinea</i>	15	21	0.33	1.20 ± 0.88	64.71 ± 22.71	22-35	1.12
<i>Hippodamia convergens</i>	16	35	0.21	-1.45 ± 1.71	107.99 ± 36.79	22-32	0.78
Meloidae							
<i>Epicauta pennsylvanica</i>	17	51	0.30	0.58 ± 0.29	70.61 ± 8.84	26-38	1.07
Cerambycidae							
<i>Pidonia ruficollis</i>	18	21	0.41	1.45 ± 0.79	55.53 ± 22.16	24-32	1.16
<i>Dectes sayi</i>	19	57	0.17	0.51 ± 0.43	76.05 ± 8.25	23-35	1.06
<i>Megacyllene robiniae</i>	20	35	0.66	1.45 ± 0.24	55.34 ± 55.34	18-32	1.16
Chrysomelidae							
<i>Diabrotica longicornis</i>	21	42	0.17	0.74 ± 0.68	80.73 ± 80.73	19-34	1.07
<i>Diabrotica undecimpunctata</i>	22	47	0.14	0.38 ± 0.41	74.01 ± 9.04	19-34	1.05
<i>Oulema melanopus</i>	23	49	0.17	0.88 ± 0.67	94.74 ± 12.16	21-33	1.08
Curculionidae							
<i>Lixus concavus</i>	24	12	0.69	1.04 ± 0.36	78.74 ± 11.38	24-39	1.18

Table 4. *Thoracic temperatures and standard deviations before and after take-off flights lasting 1–2 s*

Species	T_a (°C)	Average T_{th} before flight	Average T_{th} after flight	<i>t</i> -statistic*
<i>Popillia japonica</i>	32	36.8 ± 1.45	36.3 ± 1.46	0.927
<i>Chauliognathus pennsylvanicus</i>	25	27.2 ± 1.33	27.3 ± 1.48	0.272
<i>Coccinella septempunctata</i>	25	29.9 ± 1.81	29.5 ± 2.36	0.53
<i>Epicauta pennsylvanica</i>	27	32.2 ± 1.59	31.5 ± 2.65	0.845
<i>Diabrotica undecimpunctata</i>	25	29.7 ± 1.58	29.2 ± 1.18	1.101

* *t* at $P = 0.05$ is 2.042.

15 individuals were measured per species before take-off, and an equal number was measured after take-off.

Thermoregulation

In the five species in which thoracic temperatures were measured before and after flight, there was no significant change in temperature during the period of flight of about 1–2 s (Table 4). If it is assumed that the situation is no different in the remaining species, it can be inferred that the beetles engaged in thermoregulation during non-flight activity. Because thoracic temperature was measured before placing the beetles into the flight containers, it is likely that the beetles did not specifically engage in warm-up immediately prior to flight, but rather possessed high thoracic temperatures for some time before flight.

Dineutus americanus presents an exception, being the only beetle species in the current study observed to warm up actively immediately prior to flight. These whirligig beetles only flew over a very narrow range of thoracic temperatures (28–32°C). Individuals were observed to warm up actively to these temperatures by shivering or to cool down if placed at temperatures higher than 32–33°C [probably by evapotranspiration, because their ability to cool down ended after prolonged (10–15 min) water-free exposure to high temperatures (J. J. Oertli, unpublished observation)]. Therefore, it seems appropriate to consider the remaining species, all belonging to the suborder Polyphaga, separately. Table 5 illustrates the radically different response of *Dineutus americanus*.

The present study uses a plot of thoracic temperature against ambient temperature as an index of the precision of thermoregulation. If species had slopes paralleling $T_{th} = T_a$ or possessing a value close to one, they were considered to be thermal conformers, regardless of the amount of endothermic heat produced which, in turn, is described by the distance between the regression slope and $T_{th} = T_a$. Species with regression slopes deviating from $T_{th} = T_a$ and approaching a slope of zero were considered to be thermoregulators. The slope of T_{th} on T_a can thus be used as an index of thermoregulation. The regression equations from which these slopes were calculated are given in Table 5, and the slopes for two species displaying different degrees of thermoregulation are illustrated in Fig. 6.

Beetles with higher average wing beat frequencies were the more precise

Table 5. Regression equations and standard errors for thoracic temperature as a function of ambient temperature

Species	Ref. no.	N	Correlation coefficient	Slope	y-intercept
Gyrinidae					
<i>Dineutus americanus</i>	1	29	0.11	-0.01 ± 0.17	31.83 ± 1.31
Scarabaeidae					
<i>Diplotaxis frondicola</i>	2	50	0.94	0.97 ± 0.15	2.79 ± 3.59
<i>Hoplia limbata</i>	3	20	(T _a not measured)		
<i>Phyllophaga ephelida</i>	4	25	0.95	0.90 ± 0.09	8.26 ± 1.29
<i>Popillia japonica</i>	5	100	0.33	0.27 ± 0.27	25.80 ± 1.33
Elateridae					
<i>Ctenicera</i> sp.	6	10	0.61	0.63 ± 0.28	14.98 ± 6.79
<i>Agriotes</i> sp.	7	17	0.79	0.63 ± 0.14	14.63 ± 3.52
Cantharidae					
<i>Chauliognathus pennsylvanicus</i>	8	102	0.95	0.84 ± 0.02	6.73 ± 1.31
<i>Chauliognathus marginatus</i>	9	12	0.98	1.44 ± 0.09	-8.69 ± 2.40
<i>Cantharis bilineatus</i>	10	25	0.87	0.64 ± 0.08	13.92 ± 1.80
Lampyridae					
<i>Lucidota atra</i>	11	22	0.75	1.32 ± 0.44	-1.15 ± 9.67
<i>Photinus pyralis</i>	12	75	0.87	0.93 ± 0.02	4.51 ± 1.27
Coccinellidae					
<i>Coccinella septempunctata</i>	13	30	0.87	0.66 ± 0.07	12.93 ± 1.81
<i>Coleomegilla fuscilabris</i>	14	61	0.83	0.68 ± 0.03	11.43 ± 0.97
<i>Cycloneda sanguinea</i>	15	21	0.78	0.65 ± 0.13	12.98 ± 3.45
<i>Hippodamia convergens</i>	16	35	0.63	0.73 ± 0.24	8.80 ± 5.05
Meloidae					
<i>Epicauta pennsylvanica</i>	17	51	0.90	0.76 ± 0.76	10.46 ± 3.29
Cerambycidae					
<i>Pidonia ruficollis</i>	18	21	0.42	0.29 ± 0.14	24.06 ± 4.02
<i>Dectes sayi</i>	19	57	0.88	0.77 ± 0.05	9.09 ± 1.10
<i>Megacyllene robiniae</i>	20	35	0.93	0.95 ± 0.06	7.01 ± 1.71
Chrysomelidae					
<i>Diabrotica longicornis</i>	21	42	0.66	0.52 ± 0.10	15.65 ± 1.09
<i>Diabrotica undecimpunctata</i>	22	47	0.70	0.56 ± 0.08	15.31 ± 1.92
<i>Ouelma melanopus</i>	23	49	0.74	0.55 ± 0.07	14.64 ± 1.31
Curculionidae					
<i>Lixus concavus</i>	24	12	0.94	0.58 ± 0.07	17.08 ± 2.24

thermoregulators; there is a negative correlation between the average wing beat frequency and the thermoregulatory slope. (Fig. 7). Beetles with larger body masses, in turn, were generally thermal conformers, whereas beetles with lower body masses tended to be more precise in regulating their body temperature (Fig. 8).

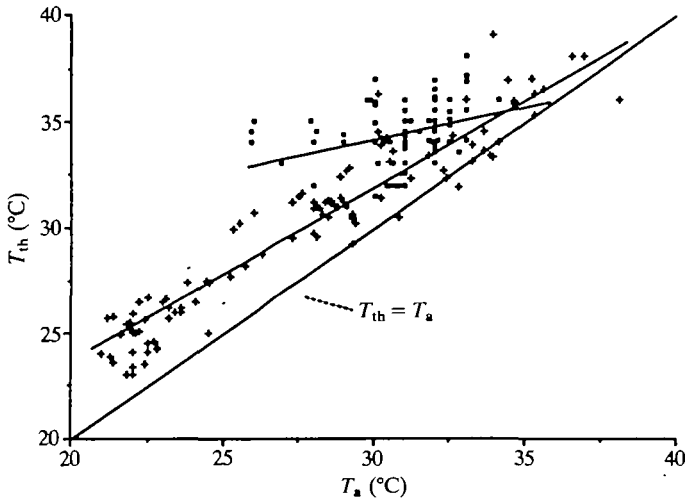


Fig. 6. Thoracic temperature (T_{th}) as a function of ambient temperature (T_a) for *Popillia japonica* (■) (linear regression equation: $y = 25.80 + 0.27x$, $r = 0.329$, $P < 0.05$) and *Chauliognathus pennsylvanicus* (+) (linear regression equation: $y = 6.73 + 0.84x$, $r = 0.950$, $P < 0.01$).

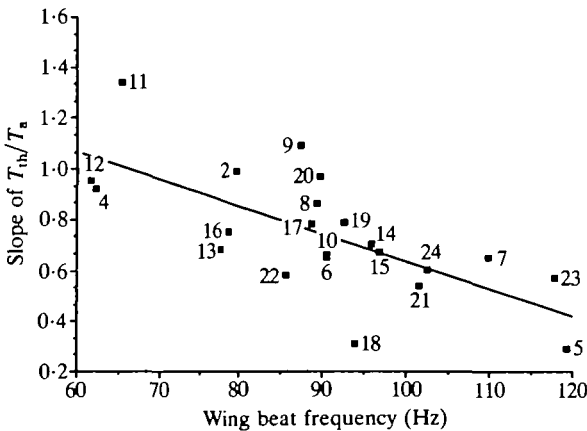


Fig. 7. Thermoregulatory precision plotted against mean wing beat frequency. Spearman rank correlation coefficient -0.715 , $P < 0.0001$.

Discussion

Temperature sensitivity of wing beat frequency

The temperature sensitivity of wing beat frequency in beetles confirms studies on other groups. May (1981) summarized available data on the influences of body temperature on frequency for both synchronous and asynchronous fliers. Fre-

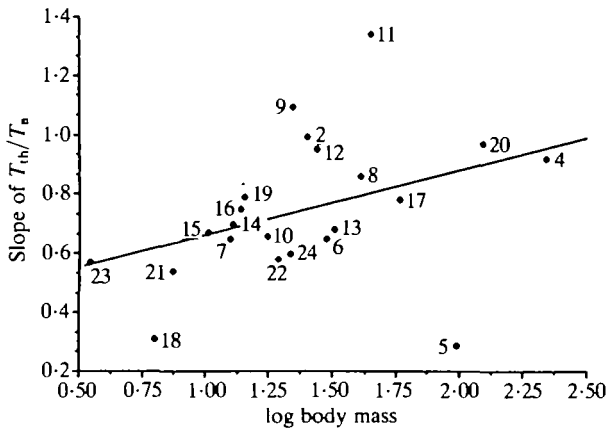


Fig. 8. Thermoregulatory precision as a function of body mass (mg). Spearman rank correlation coefficient 0.502, $P < 0.01$.

quency generally increased with Q_{10} values of 1.0–1.4. Later, a negative correlation between ambient temperature and frequency was found in certain bees (Unwin & Corbet, 1984).

The temperature sensitivity of wing beat frequency in beetles and other insects is less than that of many other biological activity rates (Prosser, 1973). In the following, I would like to discuss the various elements of the beetle flight system potentially responsible for this difference and tentatively agree with May (1981) that temperature-induced changes in the insect flight resonance system cause the observed changes in wing beat frequency over a range of temperatures.

Theoretically, three components of the flight system could be temperature-dependent: (1) the nervous system, (2) muscle metabolism (i.e. temperature sensitivity of biochemical reactions), and (3) the resonant properties of the flight system. The latter is a combination of the elastic properties of all components (cuticle, muscle, etc.) of the thorax, wing length and air viscosity. The nervous system, muscle metabolism and elastic components of the thorax have been demonstrated to change their properties over a range of temperatures (see Kammer & Heinrich, 1978; Josephson, 1981; Weis-Fogh, 1961a).

Because beetles possess asynchronous muscles, in which the frequency of contraction is not determined by the output pattern of the nervous system (Pringle, 1967, 1978), temperature sensitivity of the nervous system probably cannot be invoked to explain the effects of temperature on wing beat frequency. Circumstantial evidence of this is given by Burton (1971) and Schneider & Kramer (1974): in both reports, any change in the speed or direction of flight caused changes in the frequency of nerve impulses and corresponding changes in wing beat amplitude, although wing beat frequency remained constant.

Furthermore, if a myogenic muscle is attached to a resonant load, the oscillatory frequency of the muscle is the resonant frequency of the muscle and its load

(Machin & Pringle, 1959). If a beetle operates at resonant frequencies, muscle metabolism is a further element unlikely to be the cause for the observed frequency changes.

Therefore, the only remaining element that could be temperature-dependent is the resonant system itself. Although standard dogma, there is, nonetheless, a certain amount of controversy surrounding the validity of the contention that resonant properties determine wing beat frequency: in a forced damped oscillatory system the driving frequency determines the resulting frequency, even if it is different from the resonant frequency. However, in a harmonic oscillatory system, all deviations from the natural or resonant frequency would result in decreased amplitudes if constant power input is assumed. Conversely, if constant amplitudes are assumed, energy input must be increased. In other words, the efficiency of the oscillating system (energy required to attain a constant amplitude as a fraction of energy expended) is largest at frequencies close to the natural frequency. The reduction in amplitude, in turn, depends on the damping of the system. Russenberger & Russenberger (1963) measured a maximal amplitude change factor of 1.33 in dragonflies. If a similar value holds for beetles, a certain amount of inefficiency does occur, although the value is small enough to argue against a resonance hypothesis.

The data presented in the current study, however, supply additional circumstantial evidence favouring the resonance system as the cause of the temperature sensitivity of wing beat frequency.

The Q_{10} values of the observed frequency changes were very low, ranging from 0.8 to 1.3, much lower than the generally accepted levels for muscle metabolism of 2–3 (Josephson, 1981). Because the driving frequency determines the resulting frequency, similarly high Q_{10} values would have to be observed if changes in muscle metabolism were invoked to explain the temperature sensitivity of wing beat frequency. Josephson (1981), however, considered synchronous muscles, and the above argument is therefore based on the assumption that muscle biochemistry has similar Q_{10} values, regardless of muscle type. Interestingly, the mechanical properties of *Oryctes* (a beetle) muscle show a temperature sensitivity much closer to the wing beat frequency data presented here: specifically, the frequency at which the viscous modulus is zero increased with a Q_{10} of 1.4 for glycerinated *Oryctes* muscles (Machin *et al.* 1962). Changes in the tensile force of resilin, an important component of the elasticity of the flight system, also showed low Q_{10} values, generally in the range 1.0–1.2 (Weis-Fogh, 1961a). A higher tensile force, in turn, increases the resonant frequency of an oscillating system. In summary, the Q_{10} of temperature sensitivity of wing beat frequency in beetles is much closer to the Q_{10} observed for mechanical properties than to that of the metabolic properties of the flight system.

The observed Q_{10} values varied greatly among different species, even within the same taxonomic group. It seems reasonable to postulate that muscle metabolism will vary less among different species than will differences in the resonant properties of the thorax which, in turn, are greatly influenced by body mor-

phology. Additionally, the observed variability parallels the observations on resilin, in which Weis-Fogh (1961a) found that, at constant length, the tensile force increased linearly with absolute temperature, an identical situation to that found for frequency change in beetles. Furthermore, at higher tensile forces, achieved by increasing the extension ratio, the temperature dependence of the tensile force increased. Q_{10} ranged from 1.0 at low tensile forces to 1.2 at higher tensile forces. This result again parallels the results for temperature sensitivity of wing beat frequency presented in this paper. At higher frequencies (hypothetically caused by higher tensile forces), the thoracic temperature sensitivity of wing beat frequency increased.

In summary, these data suggest that the temperature dependence of wing beat frequency is caused by temperature-induced changes in the resonant properties of the beetle flight system and not by the temperature sensitivity of the nervous output or muscle metabolism.

The influence of wing beat frequency on thermoregulation

In five species, thoracic temperature did not significantly change during the 2 s take-off flights measured (Table 4) and T_{th} exceeded T_a . The other species, apart from *Dineutus americanus*, would probably give similar results. This indicates that thermoregulation or thermal conformity, as the case may be, occurs during non-flight activity. The precise mechanisms of warm-up are not clear, since no signs of shivering were observed. It must be stressed that non-flight activity is not the same as rest and that beetles may well have been producing more metabolic heat than during undisturbed rest. Furthermore, during regular flights after take-off, thermoregulatory precision may well change (see J. J. Oertli & M. Oertli, in preparation).

Thermoregulation, as indicated by the slope of T_{th} on T_a , correlated positively with frequency (Fig. 7) and negatively with body mass (Fig. 8).

In other taxa, higher wing beat frequencies have been demonstrated to require higher thoracic temperatures (Bartholomew, 1981). If this is also the case in beetles, it explains why beetles with higher frequencies undergo endothermic warm-up in order to increase the range of ambient temperatures over which they are able to fly. Because there was no change in thoracic temperatures over the flight period measured, differential heat production during short take-off flights cannot be invoked to explain thermoregulatory differences.

The negative relationship between thermoregulation and frequency (Fig. 8) seems counterintuitive and deserves comment. Normally larger individuals would be expected to have greater heat retention than smaller animals (Bartholomew, 1981), and would therefore be expected to thermoregulate more precisely. Obviously, however, smaller animals are capable of producing enough heat to offset losses caused by their smaller size. Additionally, the criterion for thermoregulation was the slope in the T_{th}/T_a plot and not the absolute distance of the line from $T_{th} = T_a$, which may well be larger in larger animals.

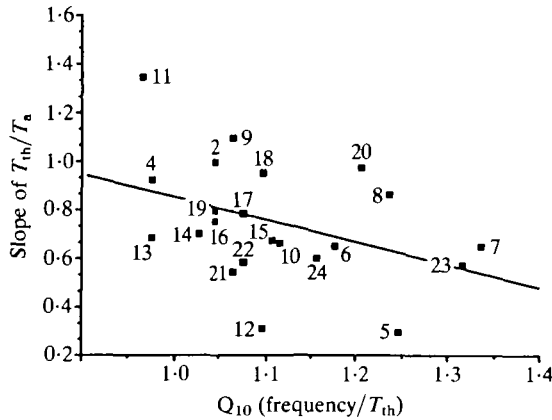


Fig. 9. Relationship between thermoregulatory precision and the sensitivity of thoracic temperature to changes in wing beat frequency. Spearman rank correlation coefficient -0.469 , $P < 0.05$.

Relationship between the temperature sensitivity of wing beat frequency and thermoregulation

As was discussed in the two preceding sections, both thermoregulation and the temperature dependence of wing beat frequency were strongly correlated with average wing beat frequency. This leads to an intriguing additional hypothesis. As argued earlier, the temperature sensitivity of wing beat frequency is likely to be an involuntary consequence of the resonant properties of the thorax. Furthermore, such changes in frequency decrease the amount of aerodynamic control an insect has over its flight. If such changes in frequency were disadvantageous to a beetle, it is possible that beetles would develop mechanisms to minimize such effects. Thermoregulation is such a strategy. Because of the higher thermal dependence at higher frequencies, the animals with large average frequencies would be more likely to thermoregulate so that they could maintain a smaller range of thoracic temperatures whilst flying at a given range of ambient temperatures. This situation is illustrated graphically in Fig. 9. This hypothesis is supported by the lack of a correlation between wing beat frequency and the *ambient* temperature sensitivity of wing beat frequency.

In summary, these data suggest that there is a continuum amongst beetle species in the relationship of temperature and wing beat frequency. At one extreme are beetles with high wing beat frequency, high temperature sensitivity and high thermoregulatory precision; at the other extreme are beetles with low wing beat frequency, low thermal sensitivity of frequency, and thermal conformity. High or low frequency, in turn, may have other selective advantages, perhaps influencing agility or economy of flight.

It is my pleasure to thank Drs T. Casey, M. May, B. Joos and R. Stevenson for valuable discussions and suggestions on earlier drafts of this manuscript.

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