MORPHOMETRICS, CONDUCTANCE, THORACIC TEMPERATURE, AND FLIGHT ENERGETICS OF NOCTUID AND GEOMETRID MOTHS[1]

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Geometrid moths in our sample differ from noctuid moths in that they have larger wings relative to their body and are smaller in body mass. As a consequence of their smaller mass, thoracic conductance of geometrids is greater than that of noctuids. Wing stroke frequencies increased with body mass and wing loading in both families. Therefore, it is likely that heat production during flight increases with body mass for these moths. Geometrids exhibited similar thoracic temperature excesses ($T_{th} - T_a$) of about 5–9 C, regardless of T_a between T_a's of 11 and 22 C. In noctuids, ($T_{th} - T_a$) was greater at low T_a than high T_a (12 C at $T_a = 11$ C; 7 C at $T_a = 22$ C), suggesting that thermoregulation occurs during flight. Differences in flight performance and thermoregulation were correlated with flight morphology in the two families. Geometrids are capable of immediate flight and are erratic fliers, and high levels of thoracic heat loss coupled with low levels of heat production precluded the possibility of maintaining elevated, regulated thoracic temperatures during flight. In contrast, noctuids have relatively greater rates of heat production due to their wing shape. Compared with the geometrids, the flight pattern of noctuids is energetically more expensive and requires preflight warm-up, but the flight repertoire is enhanced.

INTRODUCTION

It is well known that many insects exhibit elevated thoracic temperatures during flight due to the heat produced as a by-product of the flight effort. During the past decade, many aspects of endothermy have been examined in several insect taxa (see reviews by Heinrich 1974; Kammer and Heinrich 1978; May 1979; Bartholomew 1981; Kammer 1981). The equilibrium thoracic temperature of flying insects is related both to the rates of passive thoracic cooling and to rates of heat production. Thoracic conductance is clearly related to body size, because as body size decreases, the surface-to-volume ratio increases, thereby facilitating an increased mass-specific thoracic conductance in smaller insects (Bartholomew and Epting 1975; May 1976). Insects from a wide range of morphological types, including dragonflies, bees, flies, and moths, have generally similar thoracic conductance for any given thoracic mass (May 1976; Bartholomew 1981; Casey, Hegel, and Buser 1981). Heat production, however, does not exhibit such a strong dependence on body size because the heat produced during flight is a by-product of power requirements which are dependent not on size per se but, rather, on the aerodynamic configuration of the insect (Weis-Fogh 1973; Casey 1981*b*, 1981*c*). For example, the gypsy moth (*Lymantria dispar:* Lymantriidae) and the eastern tent caterpillar moth (*Malacosoma americanum:* Lasiocampidae) are similar in body mass but differ significantly in wing morphology. As a consequence, flight metabolism of *M. americanum* is about two and one-half times greater than flight metabolism of *L. dispar,* and flight temperatures of the two species are affected differently by ambient temperature (Casey 1980, 1981*a*).

The present study examines the thoracic flight temperatures of moths of the two large macrolepidopteran families, Geometridae and Noctuidae. These moths

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are particularly interesting because their small body masses (50–250 mg) result in a relatively high thoracic conductance. In addition, the wing morphology and thoracic temperatures of these groups differ significantly (Bartholomew and Heinrich 1973). Our study also relates differences in morphology to heat production and heat loss during flight.

MATERIAL AND METHODS

Moths were collected in the Hutcheson Memorial Forest, Somerset County, New Jersey, by attracting them to a 15-W ultraviolet light placed in front of a white sheet. Field experiments were conducted between 2200 and 0100 hours (EDT) during August 1979. Ambient temperature (T_a) ranged from about 11 C to 22 C.

FIELD EXPERIMENTS

The moths were captured while flying toward the sheet and were immediately placed in one of several small glass containers of different sizes. Under most circumstances they continued to fly within this confined space. Wing stroke frequency *(n)* was recorded using a Sony portable tape recorder by placing a directional microphone at the mouth of the container. Thoracic temperature (T_{th}) was measured immediately after n was recorded. The T_{th} was measured using a probe consisting of a 44-gauge copper-constantan thermocouple threaded into a 26-gauge hypodermic needle. The junction of the thermocouple was attached to the tip of the needle by a drop of quick-drying liquid adhesive. The probe was connected to a Bailey Instruments Laboratory thermometer, and T_{th} was measured to the nearest 0.2 C. The moths were grasped by the distal portion of the forewings, and the probe was thrust into the center of the thorax. Because of the low thermal inertia of the probe tip, temperatures stabilized within 2 s of insertion. Often after T_{th} was measured, the moths would continue to beat their wings vigorously while impaled on the temperature probe. We measured n under these conditions by placing the microphone directly below the animal such that the wing tip struck the microphone on the downstroke.

Immediately after an experiment, moths were killed by placing them in a jar saturated with either ethyl acetate or cyanide vapor. They were then weighed to the nearest 0.2 mg on a Roller-Smith Precision Balance. For transport back to the laboratory, the moths were then placed in individual numbered paper triangles which were stored at 100% relative humidity.

LABORATORY EXPERIMENTS

The following morning, 44-gauge copper-constantan thermocouples were implanted into the moths' thoraxes. Since the body mass and the hydration state of the moths was preserved, we assumed that these moths were similar to freshly killed animals. The moths were placed on index cards, and the thermocouple leads were taped to the card to facilitate movement from one thermal regime to another. The moths, with thermocouples attached, were cooled to approximately 3 C by placing them inside a constant-temperature cabinet. The index cards were transferred to a Styrofoam block at room temperature (approximately still air), and the rate of passive thoracic heating was continuously recorded by attaching the output from the laboratory thermometer to a polygraph. Thoracic heating constants *(K)* represent 2.303 × the slope of the semilog plot of ($T_{th} - T_a$) versus time. Thoracic conductance was calculated as the product of K and the specific heat (3.43 J/g/°C).

Moths were mounted and dried with wings in natural flight position (i.e., the trailing edge of the forewing was perpendicular to the body). Each moth was pinned along with a paper tag bearing a number which corresponded to the field experiment. They were then photographed together with a millimeter ruler, and photographic prints were enlarged to natural size. Wing areas were measured to the nearest 0.1 cm^2 with a planimeter. Wingspan and wing length were measured to the nearest 0.1 mm with calipers.

Thoracic mass was measured to the nearest milligram, either in the laboratory or in the field after legs, head, wings, and abdomen were removed with forceps and irridectomy scissors. No other data were collected on these individuals. Measurements were made within seconds after the moths were removed from a cyanide killing tube.

Wing stroke frequency data were reduced either by direct counting after the tape speed was reduced eightfold or the output of the tape recorder was connected to a storage oscilloscope. Single sweep duration was 200 ms, and either wing beats were counted from the stored trace or the period between wing beats was measured to the nearest 0.1 mm with calipers. Measurements of n for *Malacosoma americanum* during free flight using this technique yielded values essentially the same as measurements of n obtained from impedance electrodes implanted in the thorax (Casey et al. 1981).

Identification of specimens was either made or confirmed by Mr. Joseph Müller, R. D. 1, Lebanon, New Jersey 08833.

RESULTS

MORPHOMETRICS

The body shape of the geometrids differed from that of the noctuids. In general, geometrids have relatively smaller bodies and larger wings than the noctuids. Body mass of geometrids in our samples was about half that of the noctuids (table 1). Wing area was about the same for both families, however, yielding significantly lower wing loading for the geometrids. Wing loading was strongly correlated with body mass (table 2, fig. 1). As shown in figure 1, there was essentially a continuum between families for body mass and wing loading. The relation of wing loading for all moths regardless of family is

$$\log \text{wing load} = 0.77 \log \text{mass} + 0.18 \quad (r = .77), \quad (1)$$

where wing load is given in mg/cm^2 and body mass is in mg. The mean thoracic masses of the geometrids and noctuids were 19.2 mg and 47.3 mg, respectively (table 1). This represents M_{th} which was 40% and 37% of body mass in both families. Thoracic mass showed essentially the same scaling in the two families (fig. 2).

Other morphometric parameters of geometrids and noctuids and their scaling

TABLE 1

MORPHOMETRIC PARAMETERS OF GEOMETRID AND NOCTUID MOTHS

	$\bar{X}$	SD	Range
Geometrids (no. ≥ 42):			
Mass (g)	.0635	.038	.022−.220
Wing length (mm)	17.3	2.6	1.31–2.20
Wing area (cm^2)	3.886	1.381	1.66– 6.96
Wing loading (g/cm^2)	.017	.009	.0048–.017
Thorax mass (g)	.019	.009	.008–.045
Noctuids (no. ≥ 76):			
Mass (g)	.120	.043	.040–.234
Wing length (mm)	17.6	2.7	16.0–23.7
Wing area (cm^2)	3.68	1.10	1.66– 7.40
Wing loading (g/cm^2)	.033	.011	.0099–.0675
Thoracic mass (g)	.047	.012	.015–.072

TABLE 2

COEFFICIENTS FOR THE ALLOMETRIC EQUATION[a] RELATING COMPONENTS OF WING MORPHOLOGY (Y) TO BODY MASS IN MILLIGRAMS (X)

	GEOMETRIDAE				NOCTUIDAE			
	m	b	r[b]	P	m	b	r[b]	P
Wing length (cm)	.018	.12	.44	.01	−.15	.19	.44	.01
Wing area (cm^2)	−..03	.17	.25	NS	−.28	.27	.41	.01
Wing load (mg/cm^2)	.39	.61	.64	.01	.34	.69	.68	.01

[a] $\log Y = m \log X + \log b$.

[b] r = correlation coefficient.

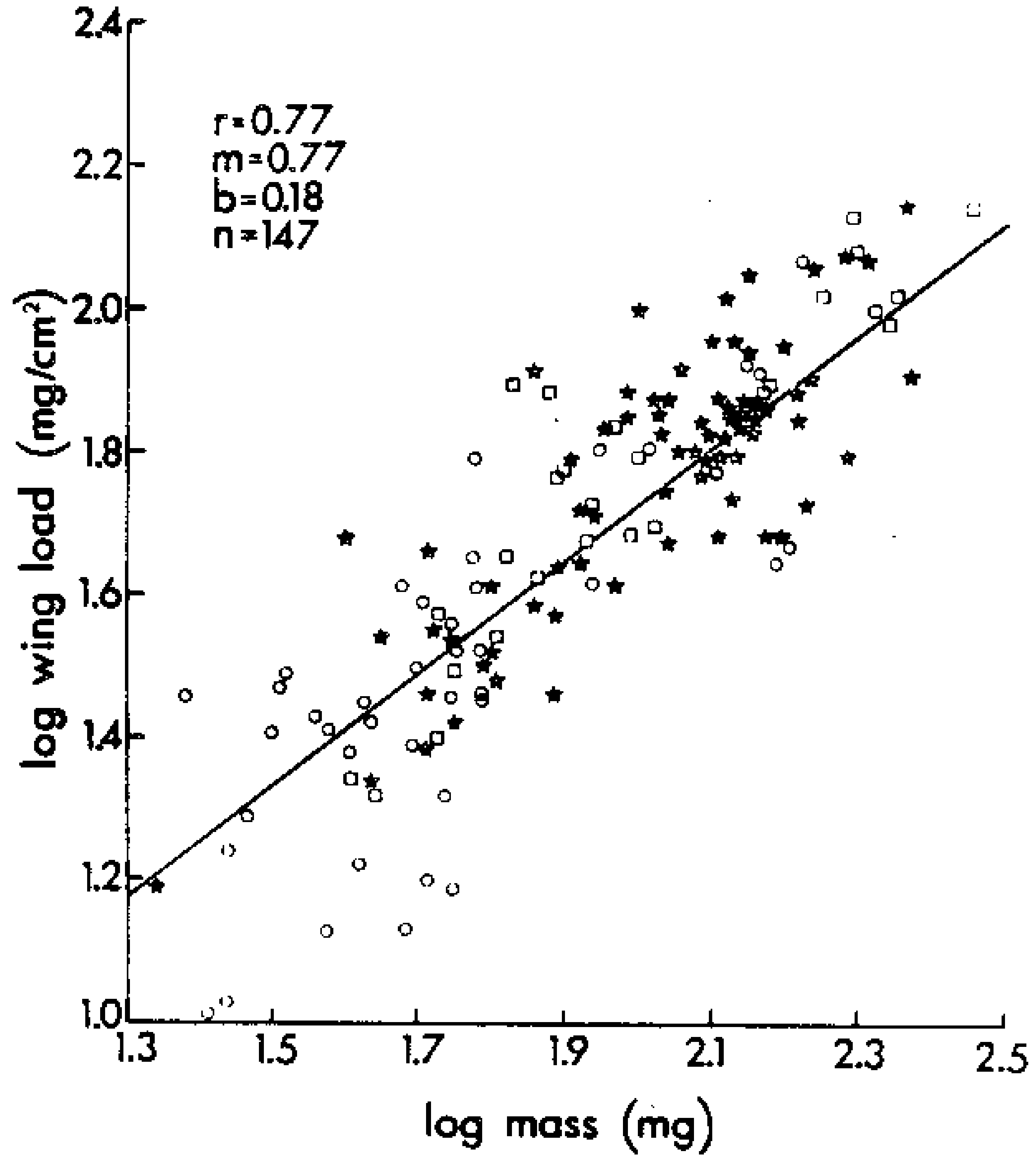

Fig. 1.—Linear regression for log transformed values of wing loading in relation to body mass in (★) noctuid moths, (○) geometrid moths, (□) other miscellaneous moths. In this and subsequent figures, r = correlation coefficient, m = slope of the linear regression, b = Y intercept, and n = sample size.

properties are given in tables 1 and 2. Within families, geometrical similarity is not apparent. If all species within a family were geometrically similar, one would predict that wing length and wing loading would scale to the one-third power of body mass, and wing area to the two-thirds power. Actual scaling coefficients for both the noctuids and geometrids (table 2) do not conform to the predicted relationships.

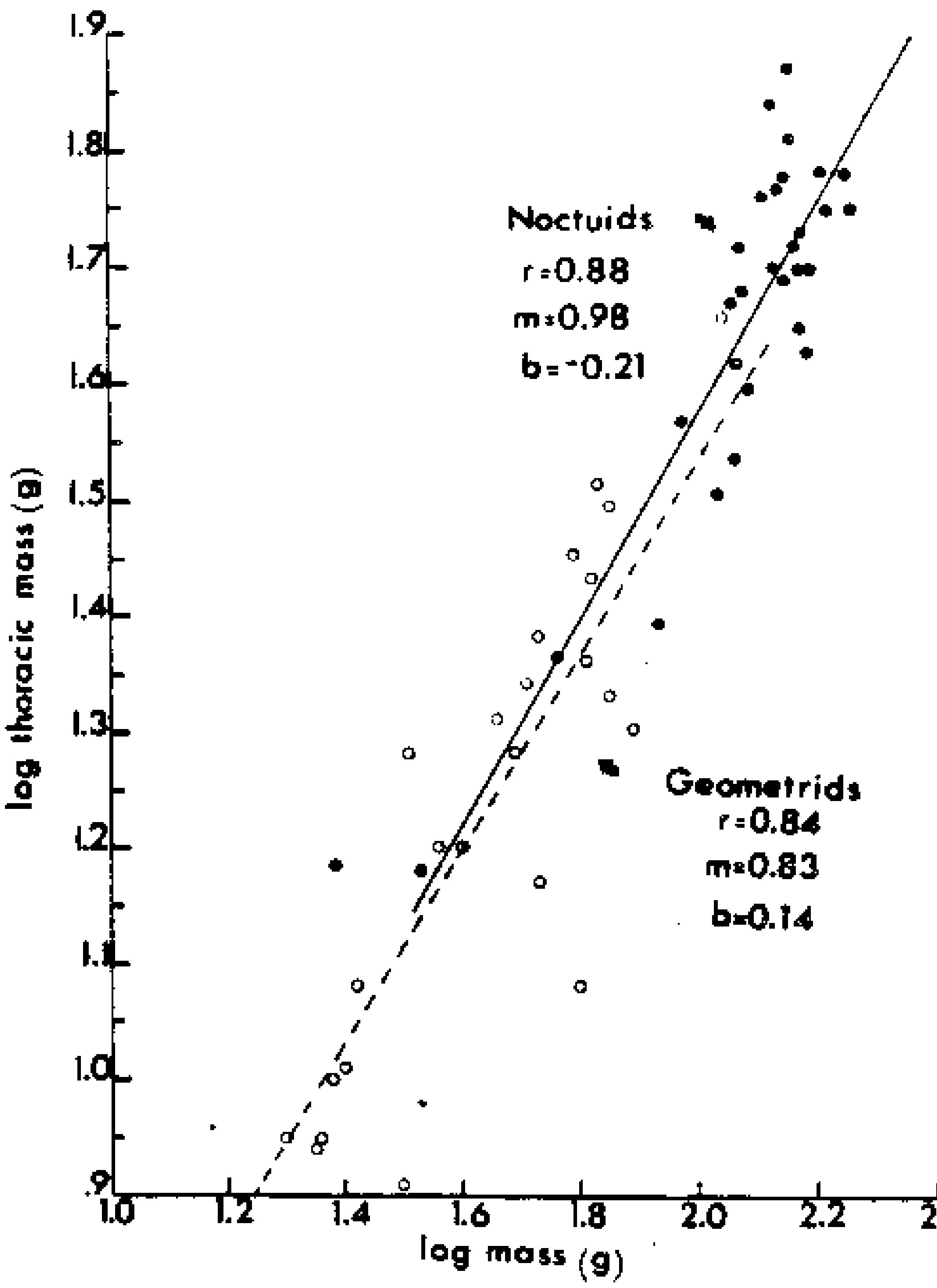

Fig. 2.—Linear regression for log transformed values of thoracic mass in relation to body mass for (○) geometrid moths and (●) noctuid moths.

THORACIC CONDUCTANCE

As in other insects, mass-specific thermal conductance of geometrids and noctuids was inversely related to body mass. For geometrids and noctuids, respectively, the equations describing the relation of thoracic conductance to body mass are

$$\log C = -0.50 \log M + 2.48 \quad (r = .80), \qquad (2)$$

and

$$\log C = -0.38 \log M + 2.21 \quad (r = .66), \qquad (3)$$

where C = mass-specific thermal conductance in W kg^{-1}°C^{-1} and M = body mass in mg. The geometrids (no. = 24) exhibited a greater increase in conductance with decreasing body mass than did the noctuids (no. = 36). In the region where body mass of the two families overlapped, conductance of geometrids was similar to that of noctuids. However, note the large scatter of data for geometrids in the 30–60-mg size range (fig. 3). Several factors may be responsible for the wide spread at low body masses. Subjectively, the geometrids appeared to be less well insulated than the noctuids, but we did not systematically examine insulation. Conduction of heat along the thermocouple wire should have a greater effect on thoracic cooling constants of the smallest specimens, but in view of the findings of Heinrich and Pantle (1975) on syrphid flies, we doubt that this effect was significant. Finally, wings may affect thoracic cooling by altering convective heat exchange (Wasserthal 1975; Tracy, Tracy, and Dobkin 1979). Although noctuids usually died with wings folded over their backs, geometrids could have their wings folded tentlike above the thorax and abdomen or fully extended laterally. Our data are not sufficient to explain the variability at lower body masses. In view of the low correlation between conductance and body mass in the geometrids (coefficient of determination = 0.43) and the similarity of conductances in the two families where they overlap in body mass (fig. 3), as a first approximation, we assume that conductance of geometrids and noctuids is a similar function of body mass.

The relation of mass-specific conductance (W kg^{-1} $°C^{-1}$) to body mass (mg) of all moths (fig. 3) in our sample (including arctiids and notodontids) is described by the equation,

$$\log C = -0.48 \log M + 2.45 \quad (r = .81). \qquad (4)$$

This relation is similar to those derived for sphingid moths (Bartholomew and Epting 1975) and for bees, dragonflies, and tabanid flies (May 1976). The equations derived for geometrids (eq. [2]) and noctuids (eq. [3]) were generally similar to the equation (4) for all moths.

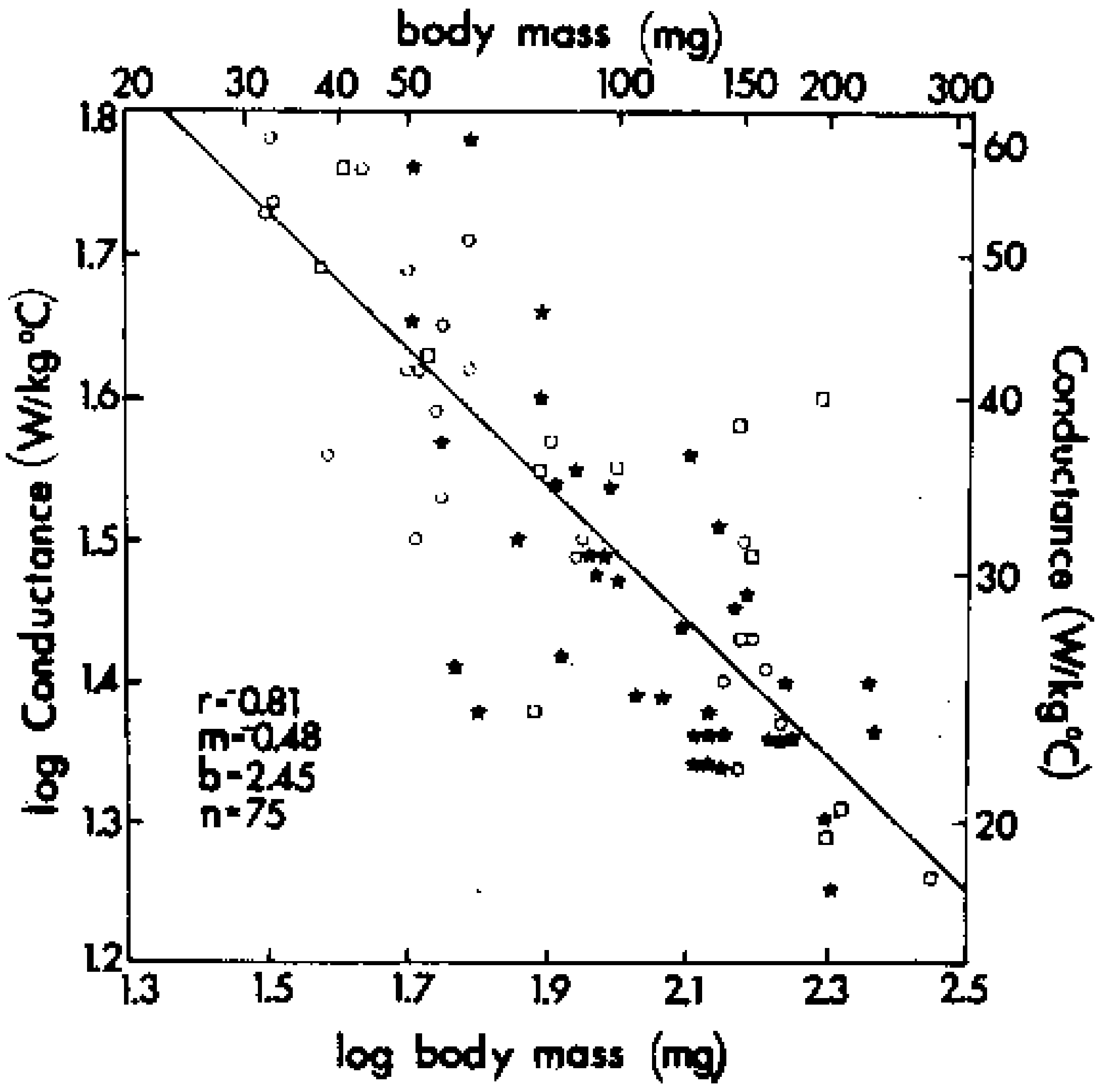

Fig. 3.—Linear regression for log transformed values of mass-specific thermal conductance in relation to body mass. Symbols as in fig. 1.

Mass-specific conductance of moths at a wind velocity of 50 cm/s was significantly greater than for moths in still air (fig. 4). The increase in slope over the still-air value (slope = −0.61) suggests that small moths were more affected by wind velocity than large moths.

WING STROKE FREQUENCY

Flight patterns of different families of moths were related to wing morphology. Noctuid, arctiid, and notodontid moths were capable of both rapid forward flight and hovering flight and exhibited a high degree of maneuverability on the wing. Geometrid moths flew more erratically, seemed incapable of sustained hovering flight, and flew more slowly than moths from other families. Geometrids were ca-

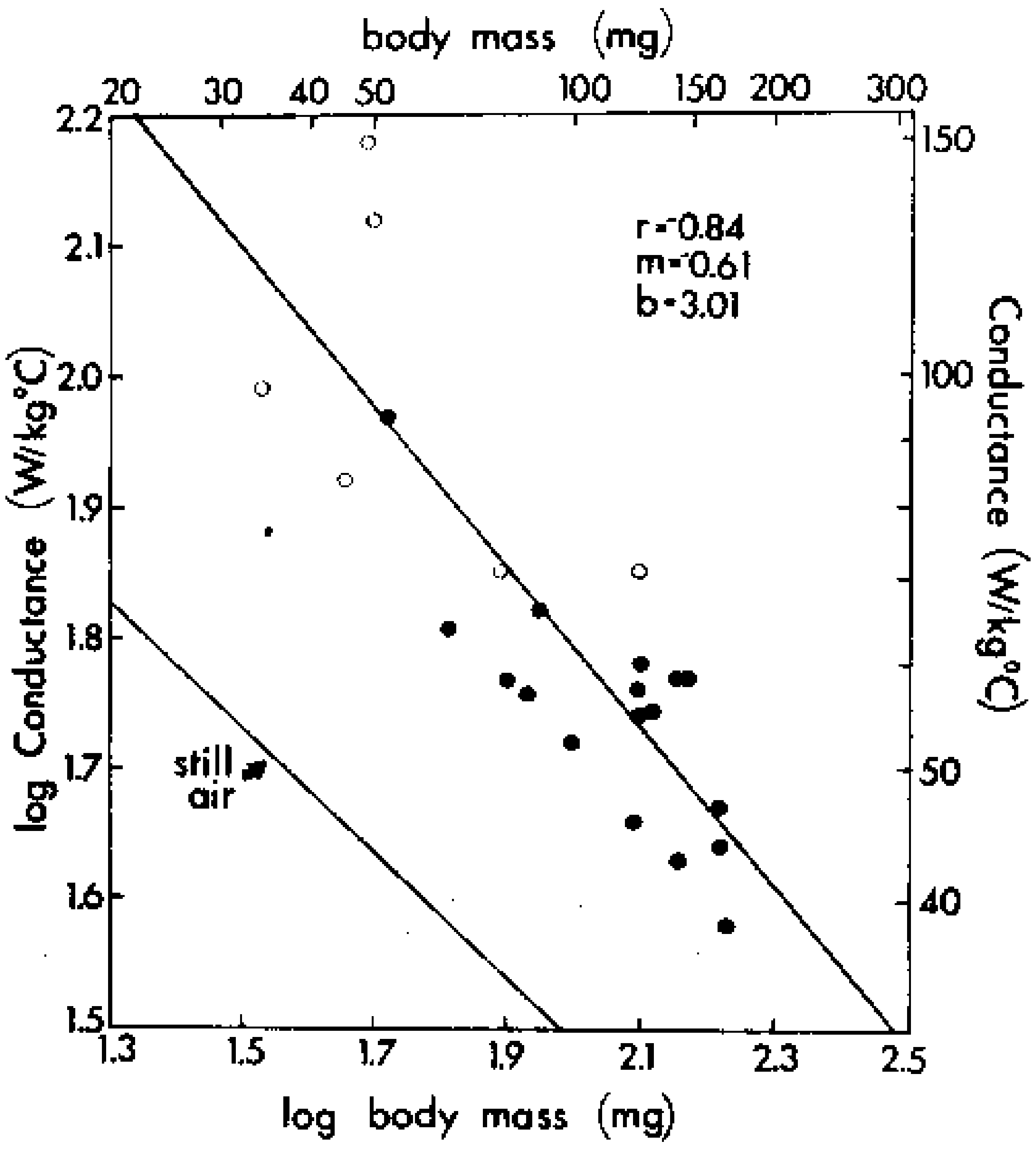

Fig. 4.—Linear regression for log transformed values of mass-specific thermal conductance for (●) noctuid and (○) geometrid moths at a wind speed of 50 cm/s. The relation for conductance vs. mass for moths in still air is taken from fig. 3.

pable of immediate flight when disturbed, regardless of the air temperature, while noctuids exhibited a period of preflight warm-up before takeoff, if they had been at rest for any length of time prior to disturbance. The wing position of the noctuids during warm-up was similar to the wing position at rest (wings folded), and only the lateral borders of the forewings vibrated visibly during warm-up.

The relations of wing stroke frequency to various morphological parameters of moths from different families are given in table 3. Few data were obtained for geometrids in free flight because these moths would not fly continuously for more than a few seconds inside the container. Presumably, this is due to their large wings and jerky, erratic movements during flight. Typically, the geometrids would collide with the walls almost immediately after takeoff and cease flight. The container needed to be shaken repeatedly in order to keep the geometrids airborne. The noctuids, on the other hand, were capable of vigorous, continuous flight within the containers.

Wing stroke frequencies (*n*) of geometrids in free flight are significantly lower than those of noctuids, arctiids, and notodontids (table 4). The *n*'s of moths in fixed flight were of similar magnitude, being slightly lower in noctuids, substantially lower in notodontids, and slightly greater in geometrids (table 3). Much of this variation is undoubtedly due to differences in sample sizes, body mass, and morphology. Therefore, we are confident that the recordings for wing stroke frequency obtained for animals in free flight did not contain harmonic frequencies which would cause significant overestimates of *n*.

Within the noctuids, *n* is not correlated with morphological parameters. Although *n* of geometrids in free flight correlates strongly with wing loading, and in fixed flight *n* correlates strongly with body mass (table 4), small sample size in this family precludes any meaningful generalization. For all moths in our sample, *n* is correlated ($P < .01$) both in free flight and fixed flight with body mass (fig. 5) and wing loading (fig. 6). However, given the low

TABLE 3

COEFFICIENTS FOR THE EQUATION[a] RELATING WING STROKE FREQUENCY TO VARIOUS MORPHOMETRIC VARIABLES

	Free Flight					Fixed Flight				
	m	*b*	*r*	*P*	No.	*m*	*b*	*r*	*P*	No.
Geometrids:										
Mass	.14	.70	.31	NS	5	.51	.42	.82	.01	9
Wing length	1.11	.75	.33	NS	5	1.36	−.27	−.13	NS	9
Wing area	1.62	−.73	−.72	NS	5	1.43	−.52	−.56	NS	9
Wing load	−.17	1.14	.98	NS	5	.88	.29	.475	NS	9
Noctuids:										
Mass	1.03	.24	.29	NS	20	1.24	.11	.15	NS	13
Wing length	1.49	.21	.11	NS	20	1.61	−.65	−.46	NS	13
Wing area	1.52	.04	.04	NS	20	1.51	−.23	−.19	NS	13
Wing load	1.10	.24	.29	NS	20	1.65	−.10	−.11	NS	13
Miscellaneous species:										
Mass	.85	.37	.70	.01	13	.46	.47	.73	.05	8
Wing length	1.82	−.92	−.46	NS	13	1.24	.76	.43	NS	8
Wing area	1.75	−.59	−.45	NS	13	1.38	.12	.21	NS	8
Wing load	1.02	.33	.54	.05	13	.71	.39	.59	NS	8
All moths:										
Mass	.95	.29	.42	.01	38	.52	.44	.70	.01	30
Wing length	1.66	−.51	−.24	NS	38	1.44	−.15	−.08	NS	30
Wing area	1.66	−.44	−.35	.05	38	1.46	.24	−.19	NS	30
Wing load	.90	.36	.56	.01	38	.82	.33	.61	.01	30

NOTE.—The symbol *m* is the slope of the linear regression of the log transformed data, *b* is the antilog of the *Y* intercept, *r* is the correlation coefficient, and *P* represents the level of significance for the regression.

[a] $\log Y = m \log X + \log b$.

coefficient of determination, it is apparent that much of the variability of wing stroke frequency is not explained by mass or by wing load. The relations between *n* and mass and wing loading are similar for moths in free and in fixed flight (figs. 5 and 6). Wing length and wing area do not significantly correlate with *n* for moths in our sample, either within or between families (table 3).

Multiple regression equations relating wing stroke frequency of various moths during free and fixed flight to wing length, body mass, and wing loading are given in table 5. In all cases multiple r^2 values are higher when all three parameters are related to *n* than when only two parameters are used, and in most cases correlations are better with two parameters than with any single parameter (table 3). In general, correlations were better for animals in fixed flight, but regression coefficients and

TABLE 4

WING BEAT FREQUENCY FOR MOTHS OF VARIOUS FAMILIES DURING FREE AND FIXED FLIGHT

Family	$\bar{X}$	SD	No.	Range
Noctuidae:				
Free flight..........	35.7	9.9	20	21–58
Fixed flight.........	29.7	6.8	12	19–38
Geometridae:				
Free flight..........	20.5	6.3	9	13–32
Fixed flight.........	23	6.9	5	16–31
Arctiidae:				
Free flight..........	33.2	9.8	7	21–48
Fixed flight.........	...	...	...	...
Notodontidae:				
Free flight..........	43.6	5.3	5	39–51
Fixed flight.........	30.2	7.1	3	24–38

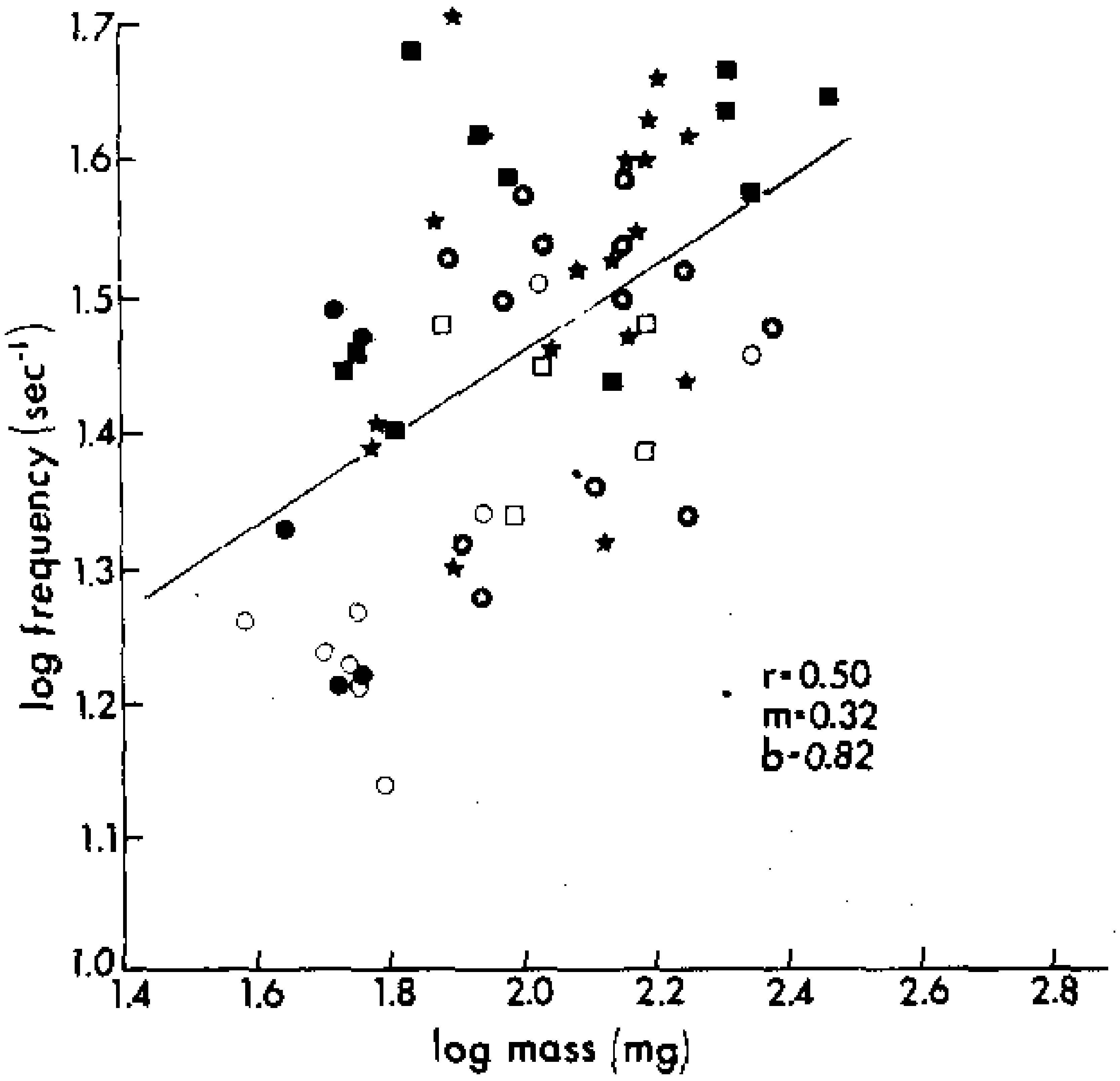

Fig. 5.—Linear regression for log transformed values of wing stroke frequency in relation to body mass for moths in free flight (shaded symbols) and fixed flight (open symbols). Circles = geometrids, stars = noctuids, squares = notodontid and arctiid moths.

multiple r^2 values could vary widely for a given family in free vs. fixed flight. The arctiids and notodontids show generally similar levels of correlation for both free and fixed flight, while the noctuids exhibited virtually no correlation in free flight and only marginal correlation in fixed flight. In view of the scatter in the data, both within and between families, the dependence of n on morphometric characters cannot be determined.

We performed multiple regression analysis to examine the effects of temperature (T_a or T_{th}) on the interrelation between n and body mass or wing loading. Since wing length and wing area were not correlated with n (table 3), we did not use these parameters in the analysis. In gen-

TABLE 5

MULTIPLE REGRESSION EQUATIONS RELATING WING STROKE FREQUENCY TO MORPHOLOGICAL PARAMETERS DURING FREE AND FIXED FLIGHT

Free flight:	
Noctuids:	
$\log n = 1.060 + .205 \log M + .192 \log l$ (±.212) (±.462)	$r^2 = .095, F = 0.84$ (±.126)
$\log n = 1.121 + .318 \log l + .185 \log WL$ (±.430) (±.206)	$r^2 = .088, F = 0.77$ (±.126)
$\log n = 1.031 + .139 \log M + .225 \log l + .087 \log WL$ (±.320 (±.491) (±.310)	$r^2 = .100, F = 0.55$ (±.130)
Arctiids, notodontids:	
$\log n = 1.02 + .361 \log M - .790 \log l$ (±.094) (±.295)	$r^2 = .687, F = 7.67$ (±.062)
$\log n = .991 - .407 \log l + .380 \log WL$ (±.171) (±.060)	$r^2 = .855, F = 20.75$ (±.042)
$\log n = .975 + .051 \log M - .469 \log l + .339 \log WL$ (±.133) (±.244) (±.125)	$r^2 = .860, F = 12.20$ (±.045)
All moths:	
$\log n = .928 + .346 \log M - .444 \log l$ (±.108) (±.299)	$r^2 = .265, F = 5.22$ (±.115)
$\log n = .937 - .353 \log l - .131 \log WL$ (±.092) (±.268)	$r^2 = .337, F = 7.38$ (±.109)
$\log n = .919 + .047 \log M - .168 \log l + .321 \log WL$ (±.202) (±.328) (±.182)	$r^2 = .338, F = 4.77$ (±.110)
Fixed flight:	
Geometrids:	
$\log n = .230 + .527 \log M + .353 \log l$ (±.150) (±.592)	$r^2 = .759, F = 6.28$ (±.083)
$\log n = .951 - .499 \log l + .323 \log WL$ (±.895) (±.260)	$r^2 = .291, F = 0.82$ (±.142)
$\log n = -.025 + .492 \log M + .133 \log l + .255 \log WL$ (±.097) (±.352) (±.098)	$r^2 = .926, F = 12.55$ (±.052)
Noctuids:	
$\log n = .570 + .563 \log M - 1.18 \log l$ (±.258) (±.416)	$r^2 = .485, F = 4.23$ (±.087)
$\log n = 1.928 - .640 \log l - .170 \log WL$ (±.415) (±.353)	$r^2 = .232, F = 1.36$ (±.105)
$\log n = 1.224 + .849 \log M - 1.39 \log l - .643 \log WL$ (±.242) (±.349) (±.271)	$r^2 = .698, F = 6.27$ (±.070)
Arctiids, notodontids:	
$\log n = .668 + .091 \log M + 2.11 \log l$ (±.372) (±1.51)	$r^2 = .810, F = 6.42$ (±.092)
$\log n = .660 + 2.18 \log l + .098 \log WL$ (±.919) (±.232)	$r^2 = .818, F = 6.73$ (±.090)
$\log n = 1.171 - 1.210 \log M + 4.53 \log l + 0.850 \log WL$ (±1.82) (±3.69) (±1.16)	$r^2 = .851, F = 3.79$ (±.100)
All moths:	
$\log n = .416 + .560 \log M - .580 \log l$ (±.104) (±.306)	$r^2 = .565, F = 14.29$ (±.099)
$\log n = .868 - .331 \log l + .355 \log WL$ (±.360) (±.100)	$r^2 = .365, F = 6.31$ (±.120)
$\log n = .375 + .450 \log M - .585 \log l + .152 \log WL$ (±.124) (±.297) (±.098)	$r^2 = .610, F = 10.95$ (±.096)

NOTE.—Values below regression coefficients represent SE. Values below r^2 represent the standard error of estimate. n = wing stroke frequency (s^{-1}), l = wing length (cm), M = body mass (mg), WL = wing loading (mg/cm^2).

eral, for geometrids, noctuids, and notodontids, multiple r^2 values for regressions were < .35. In two cases (n vs. body mass and T_{th} [all tethered moths]), multiple r^2s were .49 and .47. It is apparent that most of the variability in wing stroke frequency within and between families is not due to temperature.

THORACIC FLIGHT TEMPERATURE

In general, the difference between thoracic and ambient temperature (ΔT) in-

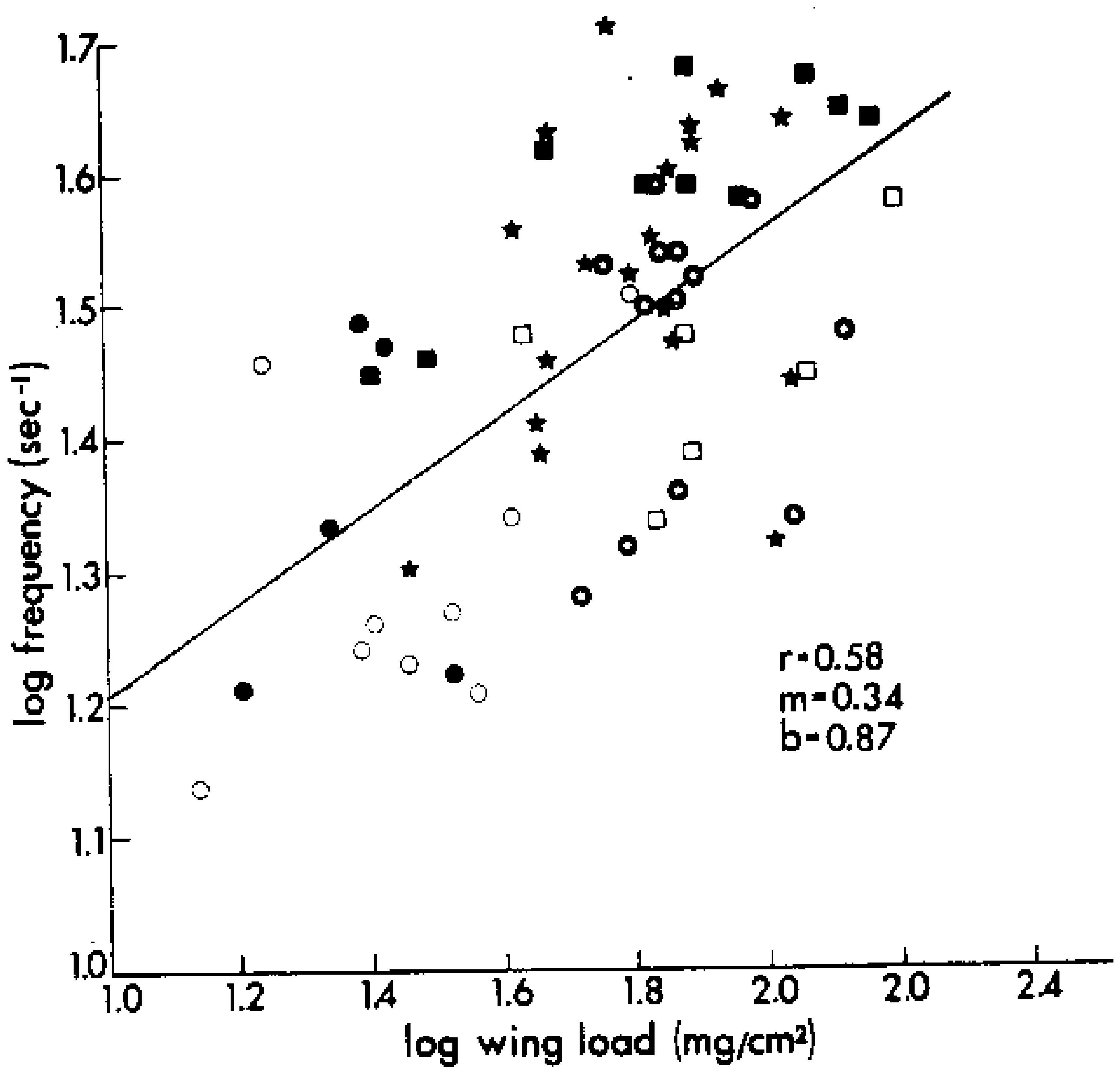

Fig. 6.—Linear regression for log transformed values of wing stroke frequency in relation to wing loading. Symbols as in fig. 5.

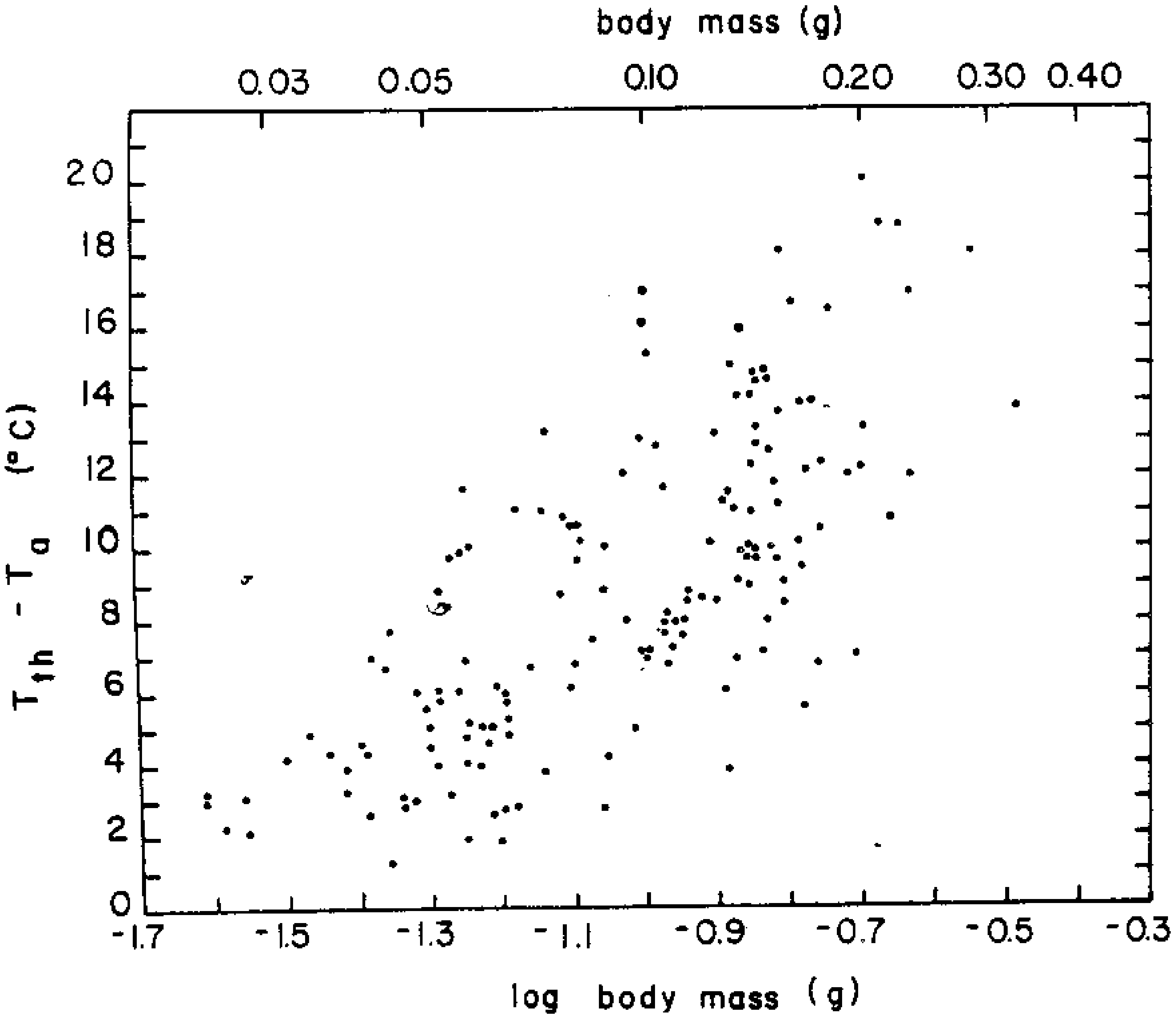

Fig. 7.—The relation of thoracic temperature excess to the log of body mass

creased directly with body mass (fig. 7). Mean T_{th} of all geometrids was lower than mean T_{th} of the noctuids (table 6) and shows a somewhat different relation to body mass (fig. 8). The large range of thoracic temperatures of the moths may be the result of the 11 C variation of ambient temperature during the study.

The relation of T_{th} to T_a differed in the two families. Geometrids showed essentially the same ΔT at all ambient temperatures (fig. 9*a*). The linear regression of T_{th} vs. T_a parallels the isothermal line, and the slope of this relation (1.1) is essentially the same as 1.0. Although geometrids elevate thoracic temperature during flight, they do not appear to regulate it. In contrast, the noctuids exhibit higher ΔT's at low T_a (fig. 9*b*). The slope of the linear regression of T_{th} vs. T_a is 0.57, significantly different from 1.0. These data confirm the findings of Bartholomew and Heinrich (1973) that noctuids have some capacity for thermoregulation during flight.

To analyze further the effects of ambient temperature on T_{th}, we chose three common species which differed significantly in size and wing loading. The results are shown in figure 10. In *Pero*

TABLE 6

THORACIC TEMPERATURE AND THORACIC TEMPERATURE EXCESS ($T_{th} - T_a$) OF NOCTUID AND GEOMETRID MOTHS AT AIR TEMPERATURES RANGING FROM 10 TO 22 C

Family and Temperature (° C)	$\bar{X}$	SD	Range
Noctuidae:			
T_{th}	26.1	3.5	17.0–34.2
$T_{th} - T_a$	10.2	3.5	3.0–18.2
Geometridae:			
T_{th}	21.0	4.7	14.0–33.0
$T_{th} - T_a$	5.6	2.9	1.9–14.0

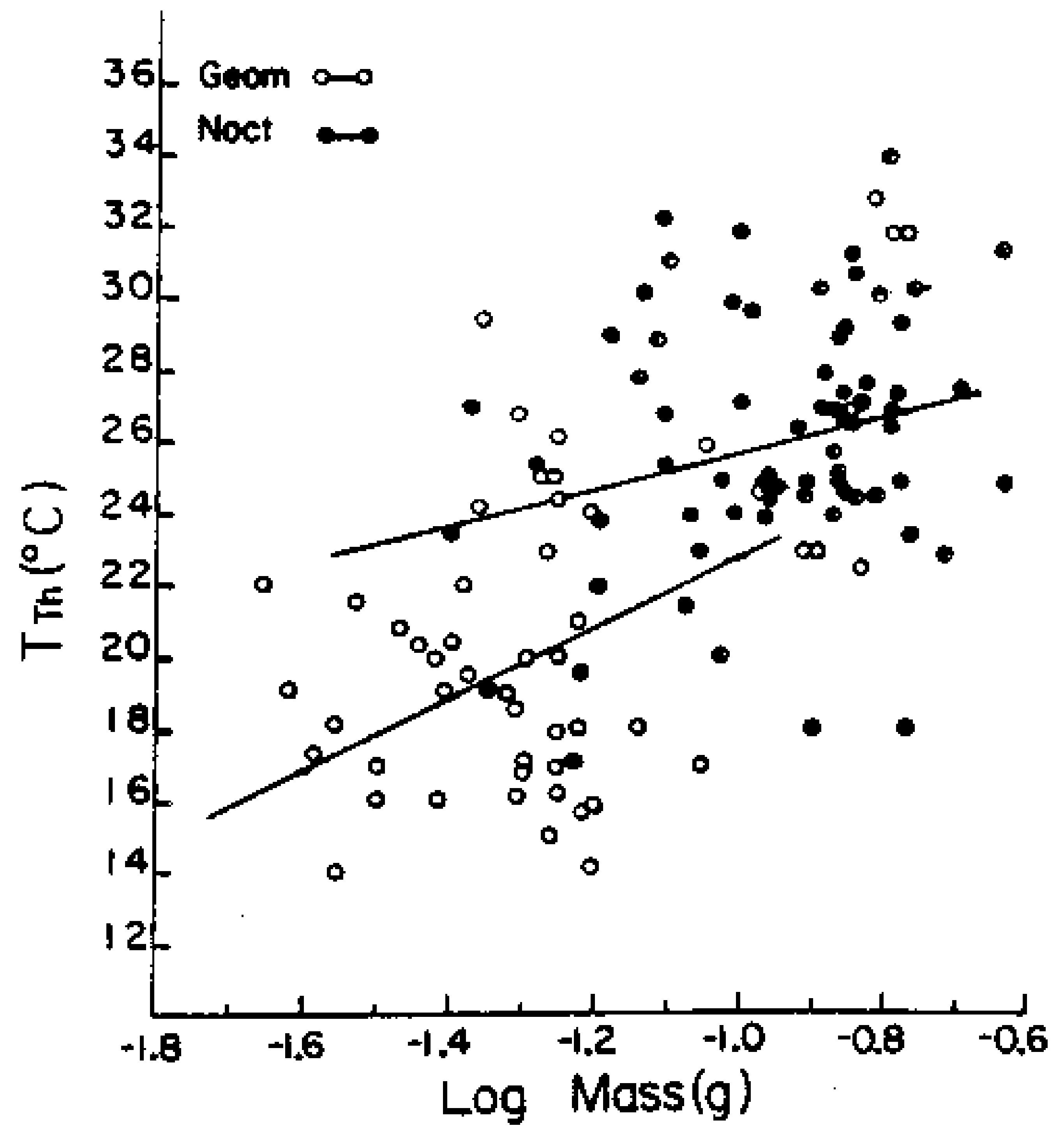

Fig. 8.—The relation of thoracic temperature to body mass in (O) geometrid and (●) noctuid moths.

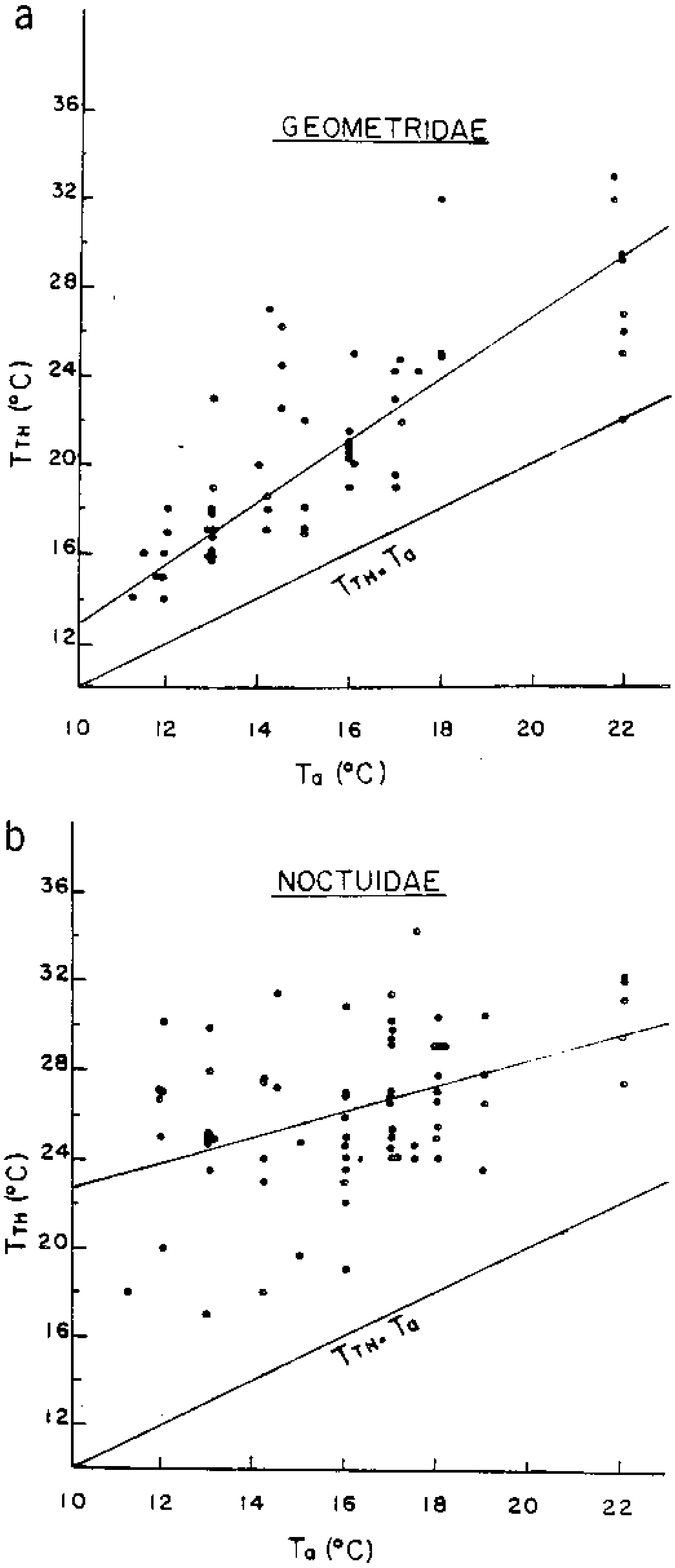

Fig. 9.—*a*, The relation of thoracic temperature to ambient temperature in geometrid moths. *b*, The relation of thoracic temperature to ambient temperature in noctuid moths.

honestarium (Wlk.) (Geometridae: mean mass = 53 mg, mean wing load = 35 mg/cm^2), mean ΔT was only 6.3 C (+ 3.1 SD, no. = 16) and similar at all T_a's. In *Amphidases* spp., the largest geometrid genus in our sample (mean mass = 145 mg, mean wing load = 65 mg/cm^2), the mean ΔT was significantly greater (9.3 C) than in *P. honestarium,* but thoracic temperature still parallels the isothermal line (fig. 10*b*). In the noctuid *Heliothis obsolita* (Fabr.), which is generally similar in size to *Amphidaes* spp. but has higher wing loading (mean mass = 141 mg, mean wing loading = 74 mg/cm^2), the ΔT decreases from about 12 C at T_a = 12 C to about 7 C at T_a = 22 C.

DISCUSSION

MORPHOLOGY AND WING STROKE FREQUENCY

When all flying animals are examined, some obvious generalizations can be made concerning the correlation between stroke frequency and wing morphology. For geometrically similar insects and birds, *n* scales with wing length to the −1 to −1.1 power (i.e., mass to the −0.33 power) (Greenewalt 1962, 1975). However, Greenewalt needed to subdivide the insects into several different groups with progressively larger wing areas per unit wing length in order to demonstrate this correlation, owing to the absence of geometrical similarity. Within the Lepidoptera, it is clear that geometrical similarity does not occur, and therefore the lack of correlation between *n* and wing length (table 3) in our sample is not surprising. When wing stroke frequency of all Lepidoptera (excluding Sphingidae, see below) are examined, it is apparent that there is a significant (albeit weak) interrelation between the wing stroke frequency and the wing loading (fig. 6) as originally predicted by Dorsett (1962). Since there is a direct relation between body size and wing loading (fig. 1; Bartholomew and Heinrich [1973]), the wing stroke frequency of moths decreases as body size decreases in contrast to the general pattern seen in other flying animals (Greenewalt 1962; May 1981). Of course, within any given size range, differences in wing size and shape are correlated with differences in wing stroke frequency and energy metabolism (e.g., within sphingids [Casey 1976]; sphingid moths vs. saturniid moths [Bartholomew and Casey 1978]; lymantriid moths vs. lasiocampid moths [Casey 1980, 1981*b*]; different taxa of euglossine bees [Casey and May 1982]).

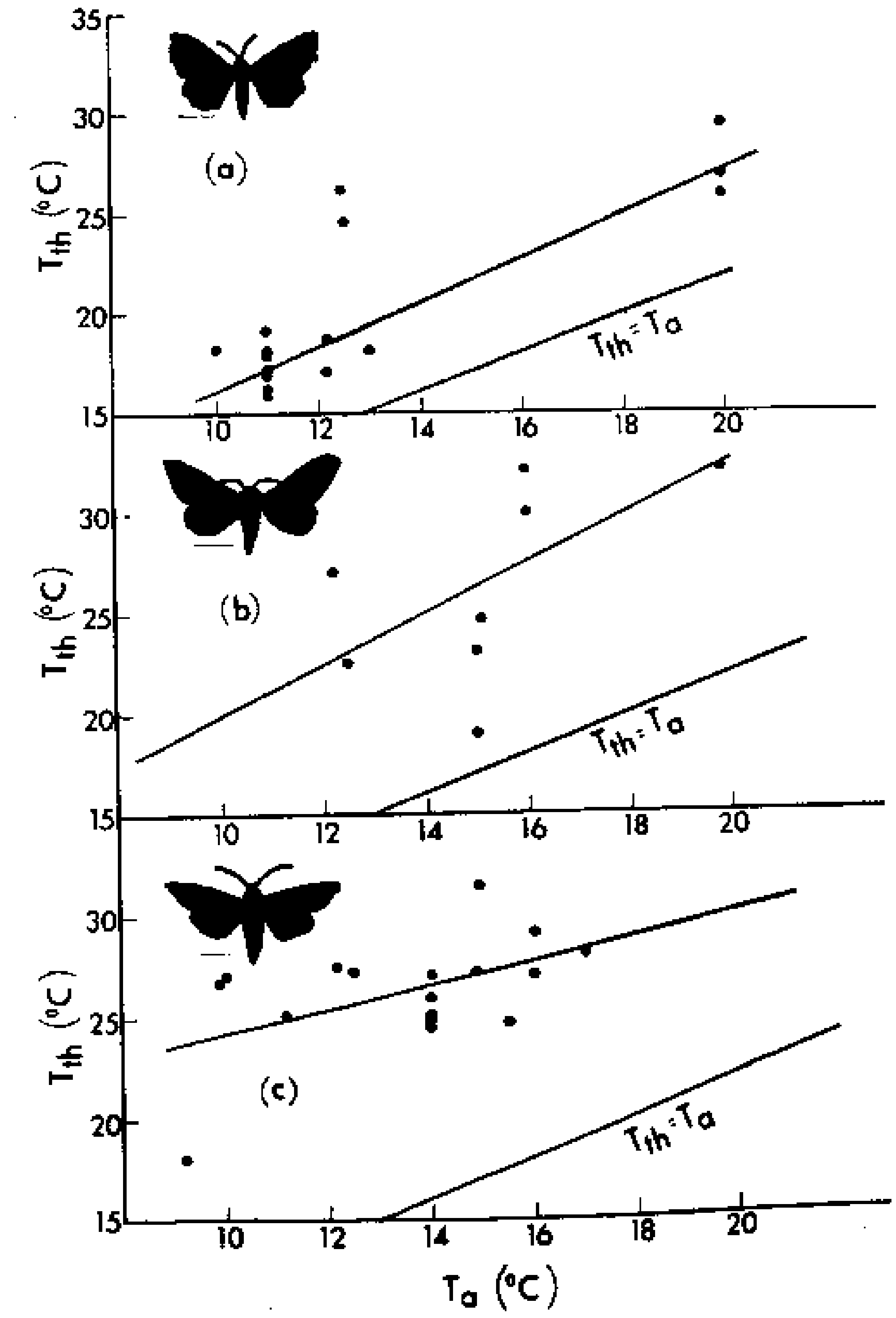

Fig. 10.—The relation of thoracic temperature to ambient temperature in three species of moths differing in size and shape: *a, Pera honestarium* WLK (Geometridae); *b, Amphidases* spp., (Geometridae); *c, Heliothis obsolita* Fabr. (Noctuidae). Horizontal bars beneath silhouettes of moths equal 1 cm.

Other things being equal, a large wing will produce more lift per wing stroke than a small wing. Therefore, moths having lower wing loads should operate at lower wing stroke frequencies. In addition, a reduction in stroke frequency may be energetically beneficial because it should reduce inertial power requirements (Sotavalta 1947, 1954). Assuming that mechanical efficiency of flight muscle is independent of size, comparison of flight metabolism with mechanical power requirements of moths suggests that accelerating and decelerating the wings at the extremes of the wing stroke represents a significantly greater power requirement than the cost of overcoming the aerodynamic drag forces (Casey 1981*a*).

These considerations are superficial,

and it is clear that more detailed examinations of wing movements are needed for insects having different wing morphology. Downward momentum applied to the air by the wing is not in a continuous jet but, rather, in a series of vortex rings produced during each half stroke (Ellington 1977; Rayner 1979). Large wings which beat slowly produce large vortex rings, and the time between the generation of each new ring (and hence new momentum applied to the air) during which the animal's weight is not being supported is relatively large. The result is a flight pattern in which the body mass appears to rise and fall during each stroke as the animal flies forward. Furthermore, because the forces produced in each half stroke are relatively large, a sudden change in some aerodynamic parameter (i.e., angle of attack, stroke plane angle, wing amplitude, etc.) should immediately affect the position of the body, contributing to the jerkiness of the flight pattern. In a moth with smaller wings, the vortex rings produced are smaller but more numerous, resulting in a more continuous downward airflow (approaching the momentum "jet"). This should yield smoother transitions from one aerodynamic condition to the next, yielding a more "controlled" flight pattern. Finally, within the Lepidoptera the degree of reliance on unsteady lift mechanisms varies widely. As the geometrids approach the Rhopolocera in wing loading, the roles of clap and fling mechanisms for generating lift and the role of drag could clearly be important and need to be assessed (see Ellington [1977, 1980] for further discussion).

Correlates between body size and wing size and shape should be generally applicable to other insect taxa, but this should be done with caution since in some cases flight characteristics of other groups can differ significantly. For example, we emphasize that the flight performance of the lower wing loaded geometrids is relatively erratic compared with that of the noctuids. This is not to say that all low wing loaded insects must necessarily exhibit such a flight pattern. Dragonflies exhibit superb control during both hovering and forward flight over a wide range of flight speeds despite their relatively low wing loading. These insects have higher stroke frequency than predicted by their wing loading as a consequence of long, relatively narrow wings (May 1981). Maneuverability may also be enhanced by the facts that the fore and hindwings beat out the phase and that during hovering and slow forward flight the stroke plane is more strongly inclined vertically than for most other insects (Norberg 1975).

Heat production during flight is related both to the wing stroke frequency and the work done per wing stroke. However, mass-specific stroke work in synchronous fliers is correlated with thoracic mass and independent of wing size (Casey 1981*c*). Therefore, we assume that differences in n during flight reflect differences in the rates of heat production. As body size decreases, wing loading decreases (fig. 1; Bartholomew and Heinrich [1973]), resulting in a reduction in n (fig. 6) and, by inference, in a reduction in the rate of heat production.

ADAPTIVE SIGNIFICANCE

The flight energetics of noctuids and geometrids differ substantially from one another, and the differences are a consequence of their respective sizes and shapes (table 7). The geometrids exhibit relatively high rates of heat loss due to their small size and relatively low levels of heat production due to their large wings which operate at low wing stroke frequencies. Consequently, although geometrids elevate thoracic temperatures during flight, T_{th} remains within a few °C of ambient temperature. The advantages of this pattern are that these moths are capable of immediate flight over a wide range of am-

TABLE 7

SUMMARY OF THERMAL AND FLIGHT CHARACTERISTICS FOR NOCTUID AND GEOMETRID MOTHS

	Geometrids	Noctuids
Wing loading	Low	High
Conductance	High	Low
Stroke frequency	Low	High
Flight cost	Low	High
T_{th}	Conformer	Regulator

NOTE.—Conductance is due to size (mass). Stroke frequency, flight cost, and flight pattern are due to aerodynamic configuration. T_{th} during flight is due to both factors (see text).

bient temperatures, and that flight is relatively inexpensive compared with insects which must operate at high wing stroke frequencies (see Heinrich 1981). The disadvantages of such a pattern are equally apparent when the flight performance of geometrids is examined. These moths are somewhat erratic fliers, operate over a small range of flight speeds, and (as indicated by their performance within the confines of the flight jars) appear to exhibit relatively poor control during complex flight maneuvers. The noctuids are more accomplished fliers than the geometrids. Their flight repertoire includes rapid forward flight, hovering flight, and a higher degree of maneuverability. However, the energetic cost of flight is undoubtedly greater for the noctuids than for the geometrids, and the mandatory preflight warm-up of these moths indicates that they are incapable of immediately achieving minimum wing stroke frequencies necessary for flight—therefore they may well be more exposed to predators than the geometrids.

It is of interest that the morphological patterns exhibited by the geometrids and noctuids in our study are common throughout the Macrolepidoptera. For example, in the arctiid and ctenuchid families of moths, ranging in mass from 100 to 500 mg, wing loading is directly correlated with body mass (Bartholomew and Heinrich 1973). As a consequence, within the Macrolepidoptera (excluding sphingid moths [see Greenewalt 1962; Casey 1981*a*]), as body size decreases, wing stroke frequency and heat production should also decrease (figs. 5, 6). This pattern was predicted by Dorsett (1962) and confirmed by Bartholomew and Heinrich (1973), although in neither of these studies was wing stroke frequency during free flight actually measured.

It is obvious that the foregoing generalizations have many exceptions within the Macrolepidoptera because flight morphology of different species having similar body mass varies widely. Body size per se also has a direct effect on the thermal characteristics of flight of different species because it is the major determinant of thoracic conductance. For example, the difference in thoracic flight temperatures of gypsy moths and eastern tent caterpillars is determined by their respective rates of heat production (Casey 1981*b*). When one is comparing moths of larger body mass, energetic correlations with morphology should be essentially similar to those we present for geometrids and noctuids. Saturniid moths operate at lower wing stroke frequency and energy metabolism and have lower wing loading than a sphingid moth of similar body mass (Bartholomew and Casey 1978). However, owing to the decrease in thoracic conductance associated with their greater mass, both families must thermoregulate at ecologically relevant ambient temperatures to prevent overheating caused by endogenous heat production.

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