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Interspecific scaling (relative size change) of wing beat frequency and morphometrics in flying beetles (Coleoptera)

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In 126 species of beetles (Coleoptera) average wing beat frequency (n) in free flight, body mass and length, elytron and ala length (l), and ala area were determined. The range of body mass covered four orders of magnitude. Most morphological parameters were significantly correlated with n but ala aspect ratio and ala loading did not influence n . With the exception of elytron length, all morphological parameters were geometrically similar. Wing beat frequency scaled with ala length^{-1/2}, a relationship significantly departing from that predicted by the harmonic oscillator model of GREENEWALT (1960) and WEIS-FOGH's (1977) interspecific rule ($n \propto l^{-1}$). Comparison with other insect orders indicated that geometric similarity in wing length occurred only in Coleoptera.

Based on Newton's second principle, $n \propto l^{-1/2}$ implies that beetles over the entire size range use the same wing mass specific force to drive their wings and that similar lift coefficient result. Furthermore, in order to enable $n \propto l^{-1/2}$ over a large size range, a large part of the kinetic energy of wing movement must be conserved, implying considerable elastic storage.

INTRODUCTION

This paper addresses interspecific scaling of wing beat frequency (n) with body and wing morphology in beetles. Wing beat frequency is an important component of aerodynamic lift production and is therefore closely tied to the energetic requirements of flight. Morphological constraints imposed on n vary in different taxa, which led WEIS-FOGH (1977) to describe "rules" of how n scales in relation to wing length. Similarly LIDTHILL (1977) proposed limiting conditions, based on various morphological and aerodynamic constraints, within which wing beat frequency might vary with linear dimensions.

GREENEWALT's (1962) studies indicate that n is proportional to wing length to the power of -1 . This relationship holds true for both flapping animals in general and for specific insect groups such as Vespoidea, Noctuidae, and Sphingidae, although marked deviations occur in certain groups (e.g. Odonata: MAX, 1981). WEIS-FOGH (1977) defined this relationship as the "interspecific rule".

Aside from a few scattered species, the situation has not been systematically studied in beetles. Because beetles possess several morphological peculiarities potentially important for flight, it is possible, based on LIDTHILL's (1977) theoretical treatise, that conditions diverge in this order. Among other things, beetles are distinguished by a stiff cuticle, the rigidity of which is enhanced by the fusion of the sternal and pleural apophyses (CHAPMAN, 1982), while in most other orders these are joined by muscles. The stiffness of the cuticle influences resonance properties of the flight system determining wing beat fre-

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quency (MACHIN & PRINGLE, 1959; PRINGLE, 1978). Additionally, the front wings have been modified to rigid and often heavy protective elytra that in most instances nonetheless undergo stroking motions during flight, although their contribution to lift production is small (SCHNEIDER & HERMES, 1976). The alae, the actual lift producing wings, are folded underneath the elytra in very complex manners. These folding patterns of the ala may affect the scaling between ala length parameter and wing beat frequency.

Similarity theories are often used to explain allometric data, and various authors have distinguished several types of similarity. Thus ALEXANDER (1982) discriminated among geometric, elastic and dynamic similarity, while ECONOMOS (1982) differentiated among mechanical, biological, and hydrodynamic similarity among organisms. All of these similarity theories make predictions about allometric scaling, allowing the current data set to be used to test the various predictions and determine which type of similarity best describes the situation in beetles.

The present study considers scaling of wing beat frequency of all beetles regardless of their taxonomic affinity. A further study will consider phylogenetic effects in different beetle subgroups.

MATERIALS AND METHODS

In a total of 126 species of beetles (table 1) wing beat frequency, body mass and length, elytra and ala length, and ala area were determined. In a few cases only one individual per species could be measured but usually many individuals were sampled to determine average values for a species (table 1).

All beetles were measured during 1987 and 1988. Most beetles were collected in central New Jersey, U.S.A., but the following species were measured in other geographic areas: Switzerland: *Oulema melanopus*, *Melolontha melolontha*; Canada, British Columbia: *Plateros* sp., both unidentified *Coccinellini*; U.S.A., Florida: *Diplotaxis frondicola*, *Diplotaxis atlantis*, *Hoplia limbata*, Oregon: *Cicindela* sp., Missouri: *Anomala innuba*, Colorado: both unidentified Chrysomelidae. Values given for *Chauliognathus marginatus* represent averages from four populations measured in Florida, Ohio, Kentucky, and Missouri. *Hippodamia convergens* were purchased from the Carolina Biological Supply Company.

Beetles were identified to the genus level following ARNETT (1968). Identification of eastern United States species, if possible, was based on DILLON & DILLON (1961). If individuals could not be identified to species level, but exhibited obvious morphological differences from other individuals of the same taxonomic group, these were considered separate species and denoted by letters (e.g. Scaritini sp a), Scaritini sp b) etc.; see table 1).

Wing beat frequencies were measured with an optical tachometer (UNWIN & ELLINGTON, 1979), recorded on tape and determined on a storage oscilloscope. Because beetles could not readily be observed to fly in the field, 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 on top, which in turn was placed in a larger, transparent 20 l plastic container. In most cases the beetles would climb to the top of the smaller container and then take off, usually heading toward the rim of the larger box. During this period of free flight wing beat frequency could be measured.

Tab. 1. Species averages and standard deviations for wing beat frequency and morphological parameters.

Suborder	Family	Species	n	freq Hz	mass mg	body length mm	elytra length mm	ala length mm	ala area mm ²	ala aspect ratio	ala loading mg/mm ²
(superfamily)	(subfamily)	(genus/tribe)									
Adephaga	Cicindelidae	Cicindela tranquebarica.	12	77.9 ±5.1	49.3 ±13.9	12.4 ±1.0	7.9 ±0.6	11.4 ±1.0	43.5 ±8.7	6.0	0.6
		Cicindela repada	3	77.8 ±1.1	48.0 ±12.5	13.0 ±1.2	8.6 ±0.7	12.4 ±0.8	50.3 ±4.8	6.1	0.5
		Cicindela sp.	2	81.5 ±0.2	65.5 ±2.1	13.7 ±0.9	8.8 ±0.5	12.9 ±0.2	44.5 ±5.6	7.4	0.7
	Carabacidae	Scaritini sp. a)	1	132.0	2.0	3.8	2.5	3.4	5.4	4.3	0.2
		Scaritini sp. b)	1	104.0	10.0	6.5	4.4	6.5	17.8	4.7	0.3
		Scaritini sp. c)	1	85.8	44.0	10.3	6.5	8.9	24.6	6.5	0.9
		Scaritini sp. d)	1	100.0	7.0	5.9	3.8	6.5	15.8	5.3	0.2
		Scaritini sp. e)	1	87.0	44.0	9.9	6.7	8.9	25.5	6.2	0.9
		Pterostichini sp. a)	1	88.4	20.0	7.7	5.5	7.7	20.5	5.8	0.5
		Pterostichini sp. b)	1	83.0	27.0	9.4	6.5	8.8	26.7	5.8	0.5
		Pterostichini sp. c)	1	89.5	25.0	9.2	6.4	8.6	23.5	6.3	0.5
		Pterostichini sp. d)	1	88.7	27.0	9.2	5.8	8.0	26.7	4.8	0.5
		Pterostichini sp. e)	1	98.5	19.0	9.1	5.9	8.4	30.3	4.7	0.3
		Pterostichini sp. f)	1	86.0	32.0	9.7	6.3	8.9	33.1	4.8	0.5
		Pterostichini sp. g)	1	94.7	7.0	5.9	5.1	6.1	17.5	4.3	0.2
		Pterostichini sp. h)	1	81.9	50.0	11.0	6.8	9.2	32.1	5.3	0.8
		Pterostichini sp. i)	1	114.1	15.0	6.5	4.6	5.9	13.2	5.3	0.6
		Harpalini sp.	1	72.0	42.0	10.5	6.7	10.3	37.9	5.6	0.6
		Galeritini sp. a)	1	109.3	17.0	6.4	4.3	5.3	12.3	4.6	0.7
		Galeritini sp. b)	1	79.2	30.0	9.0	6.3	9.4	34.4	5.1	0.4
	Gyrinidae	Dineutus americanus	29	73.0 ±16.0	49.0 ±7.3	11.0 ±0.6	7.7 ±0.5	10.0 ±0.6	77.6 ±11.6	2.6	0.3
Polyphaga											
Hydrophiloidea	Hydrophilidae	Tropisternus sp.	1	83.0	48.0	10.4	7.4	10.5	70.0	3.2	0.3
Staphylinoidea	Staphylinidae (Paederinae)	unid. a)	1	150.0	4.0	5.0	1.1	3.4	3.3	7.0	0.6
		unid. b)	1	152.0	3.0	5.1	1.0	3.6	4.4	6.0	0.3
		unid. c)	1	148.0	4.0	5.2	1.2	3.4	4.1	5.6	0.5
		unid. d)	1	141.0	1.5	2.9	1.2	3.6	3.5	7.4	0.2
	(Staphylinini)	Philonthus sp. a)	3	130.0 ±13.0	20.0 ±3.2	9.4 ±1.3	2.2 ±0.5	7.1 ±1.9	19.3 ±4.5	5.2	0.5
		Philonthus sp. b)	5	138.0 ±8.2	23.0 ±2.5	10.5 ±2.3	2.3 ±0.9	7.2 ±1.5	15.4 ±3.5	6.7	0.7

Scarabaeoidea	Scarabaeidae	(Scarabaeinae)	Onthophagus sp.	3	124.0 ±35.8	32.0 ±20.0	6.4 ±1.4	3.1 ±0.8	7.2 ±1.9	21.3 ±7.9	4.9	0.8
			Aphodius gran.	6	92.9 ±15.7	6.3 ±1.2	4.7 ±0.5	3.1 ±0.4	5.5 ±0.5	18.7 ±4.7	3.2	0.2
		(Aphodiinae)	Diploptaxis atlantis	1	75.4	70.0	10.0	7.7	12.7	63.9	5.0	0.5
			Diploptaxis frondicola	50	78.9 ±5.1	23.8 ±6.4	7.2 ±0.3	6.4 ±0.3	9.2 ±0.4	33.6 ±4.9	5.0	0.4
		(Melolonthinae)	Hoplia limbata	20	80.8 ±10.7	56.7 ±0.3	9.4 ±0.5	6.9 ±0.3	10.7 ±0.5	46.8 ±7.6	4.9	0.6
			Phyllophaga ephilida	25	61.6 ±6.3	205.8 ±95.9	15.4 ±0.8	11.4 ±0.2	17.6 ±0.3	185.8 ±17.0	3.3	0.6
			Melolonthini sp. a)	12	71.5 ±1.3	130.5 ±15.2	10.3 ±0.8	8.0 ±1.0	12.9 ±1.7	48.2 ±7.7	7.0	1.4
			Melolonthini sp. b)	3	72.3 ±6.2	125.8 ±16.8	9.6 ±0.5	7.1 ±0.4	11.7 ±0.8	48.4 ±12.6	5.7	1.3
			Melolontha melolontha	1	60.0	921.0	25.0	23.5	28.0	401.0	3.9	1.1
		(Rutelinae)	Anomala innuba	3	147.0 ±10.2	46.0 ±2.4	7.5 ±0.6	6.0 ±0.9	12.0 ±1.0	27.3 ±4.8	10.5	0.8
			Popillia japonica	100	118.5 ±8.9	93.2 ±19.9	10.8 ±0.7	6.0 ±0.3	10.5 ±0.5	58.6 ±5.1	3.7	0.8
		(Cetoniinae)	Cotinus nitida	2	122.0 ±4.2	512.0 ±5.6	20.5 ±0.1	14.1 ±0.0	21.8 ±0.0	160.0 ±6.6	5.9	1.6
			Euphoria sp.	1	114.0	503.0	21.3	14.8	22.8	180.0	5.8	1.4
		(Trichiinae)	Trichiotinus piger	5	112.6 ±51.5	95.0 ±9.6	10.0 ±1.9	5.5 ±0.7	9.3 ±1.1	28.4 ±4.6	6.1	1.7
Buprestoidea	Buprestidae		Actenodes	5	170.0 ±9.6	12.0 ±4.1	6.9 ±0.3	5.2 ±0.5	5.0 ±0.5	20.7 ±2.4	2.4	0.3
			Chrysobothrini sp.	5	164.0 ±12.8	14.0 ±2.4	9.9 ±0.4	8.2 ±0.7	10.0 ±1.0	35.4 ±1.9	5.7	0.2
			Argilus	4	141.0 ±19.3	11.0 ±3.0	6.3 ±0.2	4.6 ±0.1	4.4 ±0.2	11.2 ±1.4	3.4	0.5
			Argilini sp.	10	215.8 ±16.8	6.3 ±1.2	5.6 ±1.2	3.8 ±0.1	3.8 ±0.2	7.4 ±1.3	3.8	0.4
Elateroidea	Elateridae	(Elaterinae)	Ampedus linteus	6	107.0 ±8.1	21.0 ±12.1	9.4 ±0.9	7.0 ±0.7	7.5 ±0.6	24.0 ±6.8	4.7	0.4
			Ampedus sanguinipennis	1	110.3	10.0	7.8	5.5	6.4	18.1	4.5	0.3
			Ampedus sp.	1	70.6	25.0	10.2	6.8	7.1	29.2	3.4	0.4
			Ampedini sp. a)	1	86.9	45.0	13.8	10.0	10.0	41.2	4.9	0.5
			Ampedini sp. b)	1	98.0	22.0	11.3	8.0	8.3	33.5	4.1	0.3
			Limoniis griseus	2	80.0 ±24.7	30.0 ±12.7	11.0 ±1.4	8.4 ±0.4	8.7 ±1.2	35.4 ±3.5	4.3	0.4
			Ctenicera sp. a)	3	82.5 ±11.8	73.0 ±7.5	15.0 ±0.6	10.5 ±0.3	10.3 ±0.1	35.7 ±5.0	5.9	1.0
			Ctenicera sp. b)	10	90.0 ±9.3	28.4 ±12.0	10.7 ±1.6	7.9 ±1.0	8.4 ±1.4	28.9 ±10.2	4.8	0.5
			Agriotes sp.	17	109.0 ±14.2	11.9 ±6.8	8.1 ±1.1	6.1 ±1.1	5.9 ±1.0	17.3 ±4.0	4.0	0.3
			Cardiophorus gagatus	2	175.0 ±20.5	3.5 ±1.2	5.2 ±0.5	3.4 ±0.8	3.9 ±0.5	11.2 ±2.5	2.7	0.2
Cantharoidea	Lampyridae	(Lampyrinae)	Lucidota atra	22	64.7 ±7.85	42.5 ±19.67	11.1 ±1.09	10.5 ±1.26	10.5 ±1.6	64.2 ±10.7	3.4	0.3
			Lucidata sp.	1	66.2	17.0	12.9	10.6	10.0	42.9	4.7	0.2
			Pyropyga decipiens	1	93.7	13.0	8.6	6.9	7.5	21.5	5.2	0.3
			Photinus pyralis	75	60.8 ±4.88	25.9 ±8.96	11.3 ±0.91	9.5 ±0.72	9.6 ±0.7	58.2 ±6.2	3.1	0.2
			Photinus marginellus	1	95.5	15.0	8.1	6.8	7.5	26.7	4.2	0.3
			Photinus consanguineus	5	69.1 ±3.1	16.5 ±5.6	12.1 ±1.1	10.5 ±0.4	10.9 ±0.9	60.2 ±12.2	4.0	0.1
		Cantharidae										
		(Chauliognathina	Chauliognathus penn.	102	88.7 ±5.7	38.4 ±15.0	10.5 ±0.9	7.7 ±0.4	9.5 ±0.5	56.9 ±5.7	3.2	0.3
			Chauliognathus marg.	12	86.7 ±7.3	21.1 ±9.0	8.2 ±0.9	6.9 ±0.6	8.3 ±0.9	24.6 ±3.2	5.6	0.4
		(Cantharinae)	Podabrus tomentosus	6	71.6 ±4.0	35.2 ±11.2	10.4 ±0.5	7.7 ±0.3	9.3 ±0.6	34.6 ±5.1	5.0	0.5
			Cantharis lineola	12	133.5 ±15.6	7.3 ±8.3	5.0 ±0.5	4.1 ±0.3	4.9 ±0.5	10.3 ±1.3	4.7	0.4
			Cantharis bilineatus	25	89.9 ±7.9	16.7 ±7.5	7.5 ±0.4	6.1 ±0.4	7.1 ±0.3	20.8 ±4.1	4.9	0.4

		Cantharis carolinus	2	92.3 ±10.3	23.0 ±12.7	10.2 ±3.6	8.7 ±2.2	10.2 ±2.0	45.6 ±7.3	4.6	0.3
		Cantharis impressus	4	82.5 ±5.4	17.0 ±8.5	8.6 ±0.5	6.4 ±0.3	7.4 ±0.2	23.7 ±5.3	4.6	0.4
		Cantharis rectus	8	94.1 ±6.0	4.4 ±1.9	5.2 ±1.1	4.4 ±0.4	5.1 ±0.5	10.2 ±0.3	5.1	0.2
		Cantharis sp. a)	1	107.0	5.0	5.1	4.1	4.5	10.9	3.7	0.2
		Cantharis sp. b)	1	104.0	10.0	7.3	4.7	6.0	21.6	3.3	0.2
	Lycidae	Plateros sp.	3	73.0	46.0	12.3	11.1	11.7	54.8	5.0	0.4
Dermestoidea	Dermestidae	Athrenus sp.	7	169.3 ±4.08	3.4 ±1.1	2.7 ±0.5	2.4 ±0.3	3.0 ±0.5	4.4 ±1.0	4.1	0.4
Cleroidea	Cleridae	Trichodes nutalli	1	81.7	32.6	9.4	6.7	7.9	22.0	5.7	0.7
Cucujoidea	Nitulidae	Carpophilus sp.	6	182.0 ±11.3	0.6 ±0.2	2.4 ±0.1	1.3 ±0.1	3.2 ±0.3	2.4 ±0.2	8.4	0.1
		Glischrochilus fasciatus	1	113.2	8.0	5.6	3.1	5.8	15.2	4.4	0.3
	Sphindidae	Sphindus sp.	1	144.0	0.5	2.5	1.6	3.2	2.5	8.1	0.1
	Erotylidae	Megalodacne sp	3	116.3 ±24.6	8.3 ±2.3	5.6 ±0.9	3.5 ±0.0	5.2 ±0.5	14.3 ±2.5	3.8	0.3
	Coccinellidae										
		Cycloneda sanguinea	21	96.0 ±10.2	9.8 ±3.3	5.0 ±0.3	5.0 ±0.2	7.0 ±0.3	20.1 ±1.7	4.9	0.2
		Chilocoris stigma	1	130.0	3.0	2.9	2.3	4.8	8.0	5.8	0.2
		Hippodamia convergens	35	78.0 ±9.8	13.0 ±4.5	6.4 ±0.3	5.5 ±0.5	7.8 ±0.4	21.8 ±2.9	5.6	0.3
		Anatis quindecimpunctata	4	76.3 ±8.0	48.7 ±26.6	7.8 ±1.0	7.4 ±0.5	11.8 ±0.5	51.2 ±2.4	5.4	0.5
		Coccinella septem.	30	76.9 ±9.0	30.9 ±11.5	6.7 ±0.7	6.5 ±0.3	10.4 ±0.5	60.2 ±5.7	3.6	0.3
		Coleomegilla fuscilabris	61	95.2 ±10.8	12.1 ±2.9	5.7 ±0.4	4.8 ±0.3	6.6 ±0.3	18.8 ±2.4	4.6	0.3
		Adalia bipunctata	2	92.6 ±1.2	11.5 ±2.1	6.5 ±0.1	5.7 ±0.4	8.3 ±0.5	21.0 ±2.8	6.6	0.3
		Mulsantia picta	2	81.2 ±0.1	19.5 ±9.1	5.8 ±0.3	5.6 ±0.4	9.3 ±0.4	23.4 ±3.4	7.4	0.4
		Psyllobora vig.	2	129.2 ±7.3	2.5 ±1.4	2.4 ±0.2	2.4 ±0.1	4.8 ±0.1	8.0 ±1.1	5.8	0.2
		Coccinellini sp. a)	5	85.7 ±7.6	12.5 ±2.8	6.3 ±0.6	5.4 ±0.4	7.8 ±0.5	24.7 ±3.8	4.9	0.3
		Coccinellini sp. b)	11	82.6 ±3.0	12.1 ±1.8	6.4 ±1.0	5.5 ±0.7	7.2 ±1.9	19.3 ±11.4	5.3	0.3
Meloidea	Mordellidae	Mordellistena	5	145.1 ±29.1	2.5 ±1.0	3.3 ±0.6	1.5 ±0.3	2.7 ±0.6	3.2 ±0.5	4.7	0.4
	Meloidae	Epicauta pennsylvanica	51	88.1 ±6.9	55.2 ±19.4	9.5 ±2.3	8.1 ±0.6	9.9 ±0.7	60.4 ±5.1	3.3	0.5
		Epicauta frondicola	1	87.6	105.0	13.0	10.0	10.0	42.8	4.7	1.2
Crysomeloidea	Cerambycidae										
	(Prioninae)	Prionus sp.	2	68.6 ±7.4	93.0 ±5.2	23.4 ±2.4	16.9 ±0.5	21.6 ±0.7	132.7 ±24.8	7.0	0.4
	(Lepturinae)	Pidonia ruficollis	21	93.3 ±6.2	6.0 ±2.7	6.0 ±0.5	4.9 ±0.4	5.7 ±0.4	14.7 ±2.5	4.4	0.2
		Evodinus sp.	7	91.9 ±6.2	24.5 ±10.5	9.3 ±0.8	7.2 ±0.6	8.9 ±0.9	26.6 ±4.9	5.9	0.5
		unid. sp.	12	118.0 ±13.	16.6 ±13.0	8.5 ±1.5	6.0 ±1.1	7.2 ±1.1	19.7 ±5.8	5.3	0.4

(Cerambycinae)	Megacyllene robinae	35	89.0 ±10.3	116.4 ±63.6	16.8 ±2.1	12.0 ±1.2	13.5 ±1.3	101.3 ±4.6	3.6	0.6
	Callidium antennatum	2	80.2 ±2.9	77.0 ±11.3	13.5 ±1.2	9.5 ±0.9	11.2 ±0.4	39.3 ±6.8	6.3	1.0
(Lamiinae)	Dectes sayi	57	92.0 ±8.2	13.6 ±4.8	7.5 ±0.8	5.5 ±0.4	7.1 ±0.9	38.0 ±1.7	2.6	0.2
	unid. sp.	2	76.2 ±5.4	80.5 ±5.3	11.9 ±0.9	9.0 ±0.4	11.5 ±0.7	81.3 ±25.3	3.2	0.5
Chrysomelidae										
(Donaciinae)	Donacia sp.	3	119.0 ±29.6	9.7 ±2.5	7.3 ±0.1	5.3 ±0.1	6.2 ±0.7	17.1 ±5.2	4.5	0.3
	unid. sp.	1	176.2	5.0	2.1	1.9	3.1	4.2	4.6	0.6
(Orsodacninae)	Syneta ferruginea	1	71.2	17.0	8.1	5.8	8.9	27.6	5.7	0.3
(Criocerinae)	Oulema melanopus	49	116.0 ±11.7	3.3 ±1.0	5.2 ±0.2	3.9 ±0.4	5.0 ±0.2	12.8 ±0.2	3.9	0.1
	Crioceris asparagi	3	118.2 ±32.6	11.5 ±1.8	5.6 ±0.3	4.2 ±0.2	4.9 ±0.3	14.8 ±5.7	3.2	0.4
(Chlamisinae)	Chlamismus sp.	2	175.0 ±24.1	9.0 ±4.2	3.6 ±0.7	1.1 ±0.6	2.6 ±0.9	4.6 ±1.0	3.1	1.0
(Eumolpinae)	Xanthonia villosula	7	105.0 ±12.9	6.2 ±1.2	4.1 ±0.3	3.4 ±0.3	5.3 ±1.0	11.5 ±3.3	4.9	0.3
	Chrysochus auratus	18	84.6 ±4.6	43.7 ±18.0	8.9 ±0.7	7.5 ±0.6	9.5 ±0.7	32.6 ±5.5	5.5	0.7
(Chrysomelinae)	Leptinotarsa decim.	7	74.6 ±5.4	122.5 ±25.0	10.2 ±0.9	9.5 ±1.2	13.7 ±1.3	57.7 ±15.4	6.5	1.1
(Galerucinae)	Trirhabda bach.	2	82.0 ±5.6	80.0 ±7.3	11.0 ±0.8	9.8 ±0.7	11.0 ±0.8	48.6 ±3.5	5.0	0.8
	Galerucella sp.	3	92.7 ±10.1	5.7 ±1.7	4.7 ±0.7	3.5 ±0.7	4.2 ±0.9	10.6 ±0.2	3.4	0.3
	Diabrotica undecimpunc.	47	84.0 ±8.9	18.3 ±5.9	6.8 ±0.4	5.4 ±0.2	7.8 ±0.5	39.2 ±4.2	3.1	0.2
	Diabrotica longicornis	42	100.9 ±7.1	7.0 ±2.9	5.4 ±0.3	4.0 ±0.2	5.8 ±0.3	20.8 ±2.3	3.3	0.2
	Acalymma vitatus	1	100.0	8.0	5.0	4.9	6.5	21.4	3.9	0.2
	Cerotoma trifurcata	3	130.0 ±5.2	11.0 ±1.4	5.2 ±0.2	3.8 ±0.2	5.0 ±0.1	14.1 ±9.4	3.5	0.4
(Alticinae)	Chaetocnema sp.	3	126.0 ±16.8	4.8 ±2.2	3.3 ±0.6	2.9 ±0.5	5.3 ±0.4	10.6 ±1.4	5.3	0.2
	Phyllotreta sp.	2	94.5 ±20.5	2.8 ±1.1	3.5 ±0.8	3.2 ±0.7	5.0 ±0.6	13.4 ±2.7	3.7	0.1
(Hispiniae)	Microthorax sp.	1	177.0	1.0	2.5	2.4	3.3	4.2	5.2	0.1
(Cassidinae)	Metriorhynchus sp.	12	107.0 ±2.9	21.0 ±0.5	7.3 ±0.6	5.9 ±0.3	7.0 ±1.8	18.7 ±0.1	5.3	0.6
	Deloyala guttata	3	124.4 ±11.0	13.3 ±2.0	5.6 ±0.4	5.1 ±0.5	6.2 ±0.8	16.1 ±2.6	4.8	0.4
Curculionoidae										
(Attelabinae)	Curculionidae									
	Attelabus	1	156.3	7.0	3.3	2.5	5.4	11.5	5.1	0.3
(Curculioninae)	Sitona	1	97.0	10.5	5.3	4.8	5.9	12.5	5.6	0.4
	Curculioninae	3	159.0 ±29.7	6.2 ±0.7	4.0 ±0.2	2.7 ±0.2	4.1 ±0.9	9.7 ±0.25	3.5	0.3
	Lixus concavus	12	101.9 ±31.3	20.3 ±6.1	7.1 ±0.4	5.0 ±0.3	6.8 ±0.7	19.7 ±3.4	4.7	0.5
Scolytidae										
(Scolitinae)	unid. sp.	1	80.0	10.6	5.5	3.3	6.1	12.3	6.1	0.4

Because OERTLI (1989) found thoracic temperature to be an important determinant of n in certain beetle species, all beetles were measured at thoracic temperatures of 30°C ($\pm 1^{\circ}\text{C}$). In order to verify T_{th} of a preceding flight a copper-constantan thermocouple was placed into the thorax of all beetles immediately upon their arrival on the rim of the larger container. Previous studies (OERTLI, 1989) indicated no change in thoracic temperature during these short take-off flights.

After field measurements beetles were placed into airtight vials, returned to the laboratory, killed by freezing and weighed. One elytron and one ala were removed from each individual, taped to a microscope slide, and their lengths determined to the nearest 0.1 mm. Ala areas were measured by creating a still video image and subsequently enlarging and digitizing the area with a computer program (Image-Pro; Media Cybernetics Inc.). The above parameters allowed calculation of ala loading and ala aspect ratio (ELLINGTON, 1984).

Data for comparison with other insect orders (Diptera, Hymenoptera, Lepidoptera) were obtained from GREENEWALT (1962). Species averages were calculated, if information on more than one individual was available. This latter procedure differed from GREENEWALT's (1962) analysis, which included each individual separately regardless of the number of individuals per species.

RESULTS

Average wing beat frequencies, and mean body size and wing shape parameters for individual species are given in table 1. Average body masses ranged from 0.5 mg in *Sphindus* sp. to 921.0 mg in *Melolontha melolontha*, and average wing beat frequencies ranged from 60.0 Hz in *Melolontha melolontha* to 215.8 Hz in an Argilini species.

Tab. 2. Linear regression equations of \log_{10} transformed data describing morphological parameters as a function of body mass.

Parameter	Constant	Standard error	Slope	Standard error	r^2
Body length	0.436	0.021	0.346	0.016	0.799
Elytron length	0.250	0.032	0.375	0.023	0.655
Ala length	0.462	0.018	0.323	0.013	0.836
Ala area	0.552	0.037	0.644	0.027	0.818
Ala aspect ratio	0.673	0.026	0.003	0.019	0.000
Ala loading	-0.853	0.037	0.356	0.027	0.580

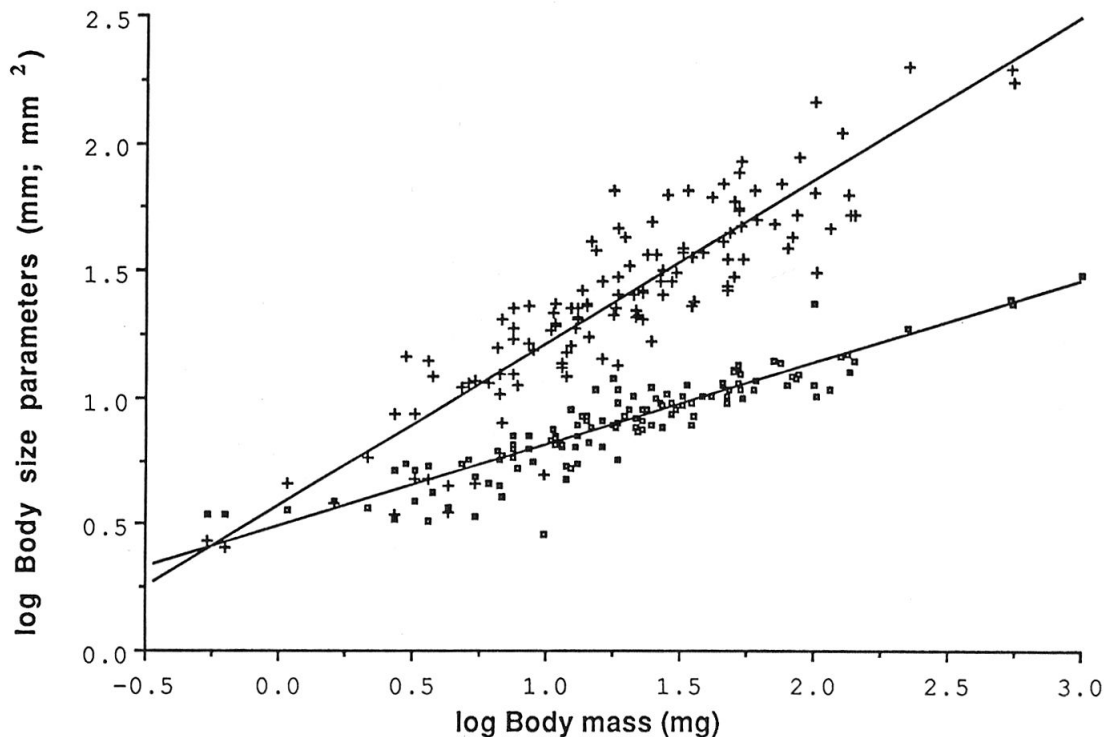


Fig. 1. Relationship of ala length, and ala area to body mass (equations given in tab. 2).

Body, elytron, and ala length and ala area were strongly correlated with body mass (table 2, fig. 1). Body length scaled with mass^{0.346} and the corresponding exponent for ala length was 0.323. Both exponents are not significantly different from $\frac{1}{3}$ ($p \leq 0.05$; test for homogeneity of regression coefficients, see STEELE & TORRIE, 1960). Elytron length scaled with mass to the power of 0.375, a value significantly larger than $\frac{1}{3}$ ($p \leq 0.05$). Body mass did not correlate with ala aspect ratio, however, ala loading scaled with body mass^{0.356}, an exponent not significantly different from $\frac{1}{3}$ ($p \leq 0.05$).

All size parameters were significantly correlated with wing beat frequency. Corresponding regression equations are given in table 3. Beetles with larger body masses, greater body lengths, longer elytra and alae, and larger ala areas had lower frequencies (figs. 2, 3). Wing beat frequency scaled with ala length^{-0.446}, an exponent not significantly different from $-\frac{1}{2}$ ($p \leq 0.05$). The scaling exponents for frequency with body length (-0.366) and elytron length (-0.348) were much lower and not significantly different from $-\frac{1}{3}$ ($p \leq 0.05$). Wing beat frequency scaled with ala area^{-0.223}, a value which in turn did not significantly differ from $-\frac{1}{4}$. Wing beat frequency scaled with body mass to the power of -0.133 . In contrast, both ala aspect ratio and ala loading were not correlated with wing beat frequency (table 3, figs. 4, 5).

In an effort to calculate the relative importance of the different morphological parameters, standard partial regression coefficients were calculated. Because all morphological size parameters were correlated with one another not all assumptions for calculating multiple regression coefficients (a first step in calculating partial coefficients) are fulfilled. However, the principle problem of multicollinearity is an increase in the standard errors of the coefficients, while the

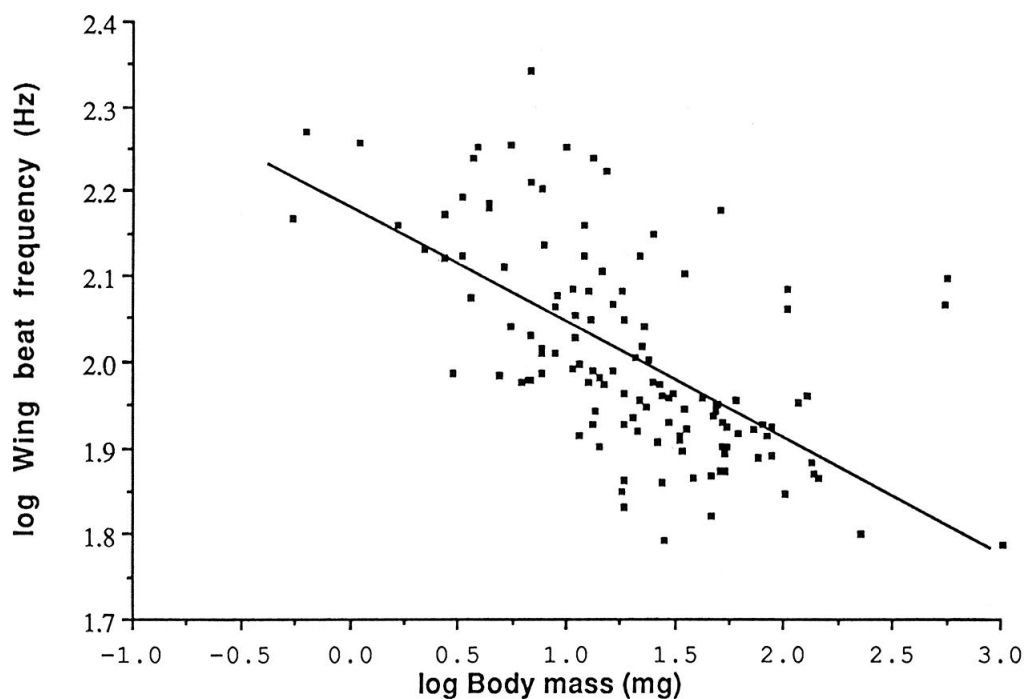


Fig. 2. Wing beat frequency as a function of body mass (equation given in tab. 3).

sample regression coefficients remain unbiased (STEELE & TORRIE, 1969), allowing calculation of similarly unbiased standard partial regression coefficients. Table 4 gives the multiple regression equation with which the largest amount of variability was explained using regression coefficients significantly different from

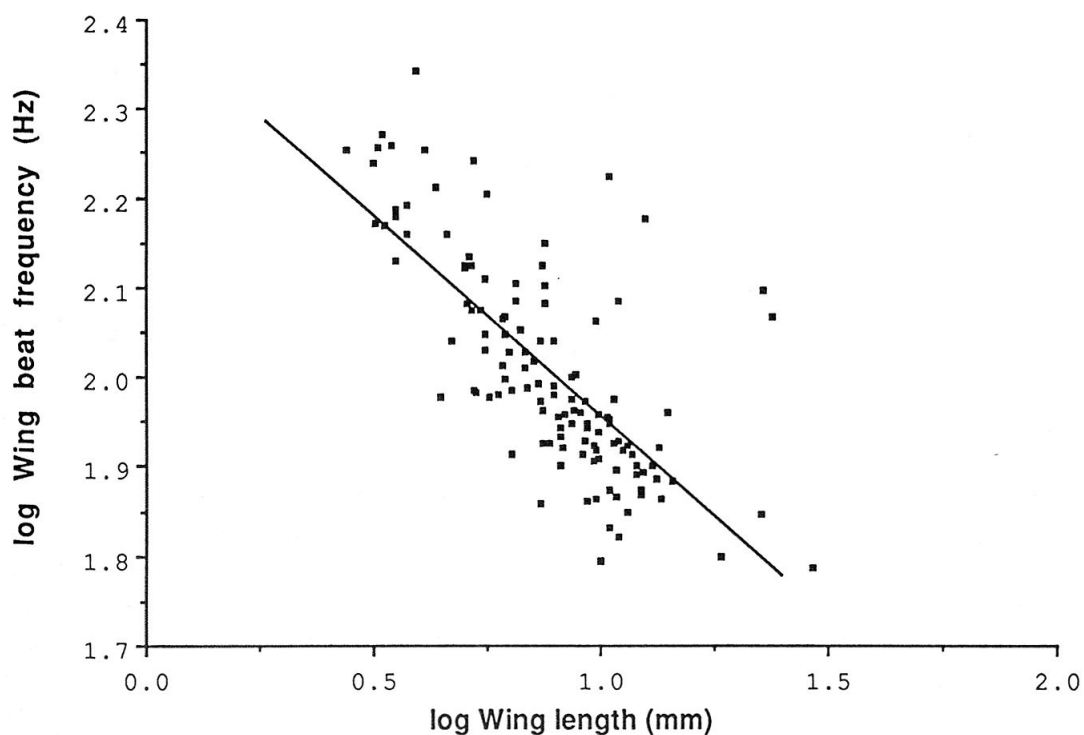


Fig. 3. Wing beat frequency plotted against ala length (equation given in tab. 3).

Tab. 3. Linear regression equations of \log_{10} transformed data describing wing beat frequency as a function of morphological parameters.

Parameter	Constant	Standard error	Slope	Standard error	r^2
Body mass	2.165	0.021	-0.133	0.015	0.375
Body length	2.316	0.034	-0.366	0.038	0.425
Elytron length	2.249	0.022	-0.348	0.029	0.537
Ala length	2.385	0.034	-0.446	0.038	0.529
Ala area	2.301	0.026	-0.223	0.019	0.535
Ala aspect ratio	1.979	0.064	0.029	0.093	0.001
Ala loading	1.061	0.020	-0.092	0.041	0.039

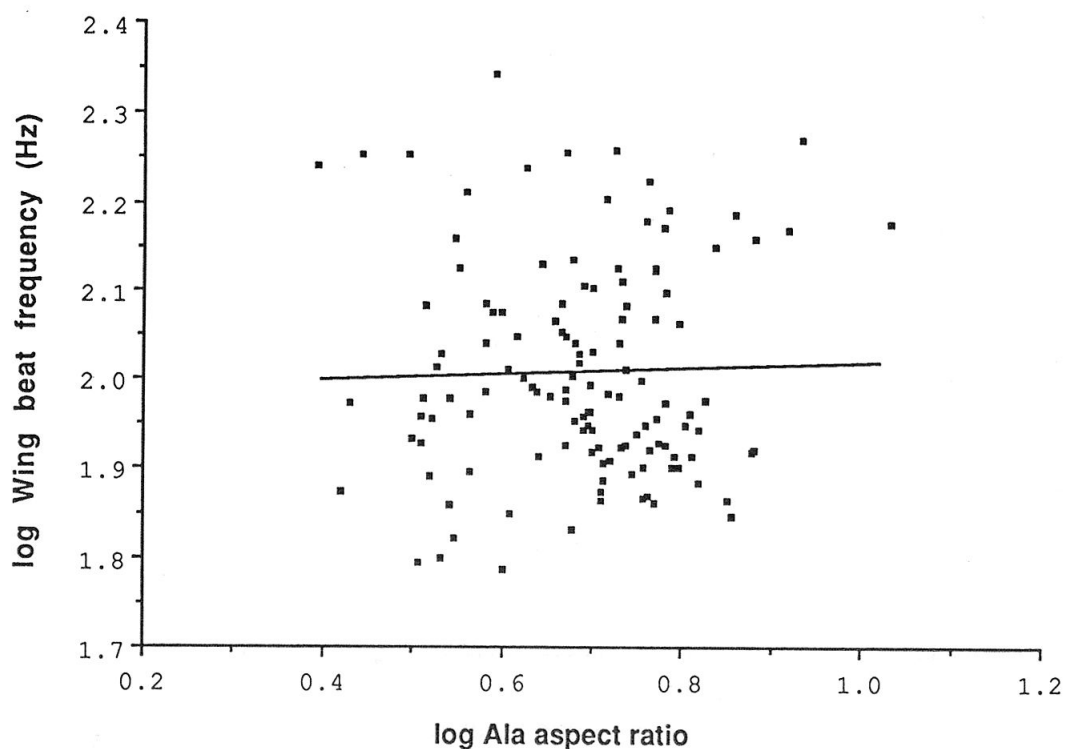


Fig. 4. Relationship of wing beat frequency and ala aspect ration (equation given in tab. 3).

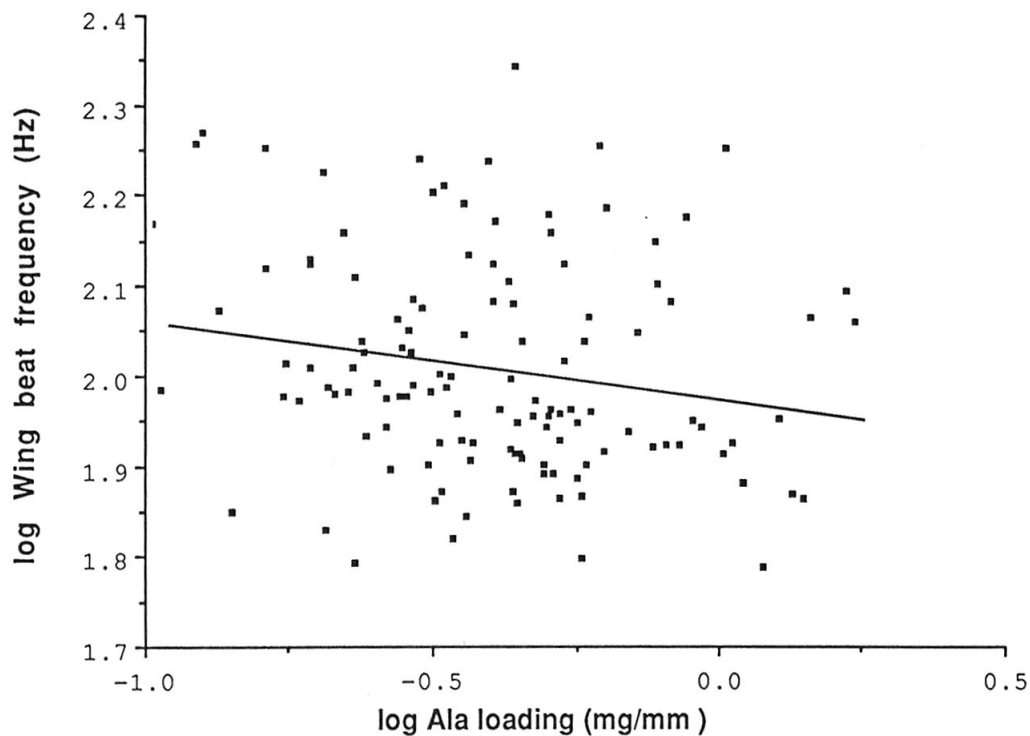


Fig. 5. Relationship of wing beat frequency and ala loading (equation given in tab. 3).

zero and the standard partial regression coefficients for these parameters. It is apparent that variations in ala length explain the largest amount of variability in frequency. Ala length is followed by elytron length, and body mass, the relative importance of these latter two parameters together is about equal to ala length (compare fig. 6).

The reanalysis of taxonomically arranged morphometric and wing beat frequency data presented by GREENEWALT (1962) indicated that in Hymenoptera wing beat frequency was proportional to wing length to the power of -0.99 , a value not significantly different from -1 ($p \leq 0.05$). In this order wing length was proportional to body mass to the power of 0.126 , significantly ($p \leq 0.05$) departing from 0.33 as predicted based on geometric similarity. In Lepidoptera, wing

Tab. 4. Multiple regression equation of \log_{10} transformed data describing wing beat frequency as a function of morphological parameters. $r^2 = 0.585$.

Parameter	Regression coefficient	Standard error	Standard partial regression coefficient
Constant	2.402	0.047	
Body mass	0.072	0.031	0.331
Elytron length	-0.199	0.061	0.417
Ala length	-0.404	0.112	0.656

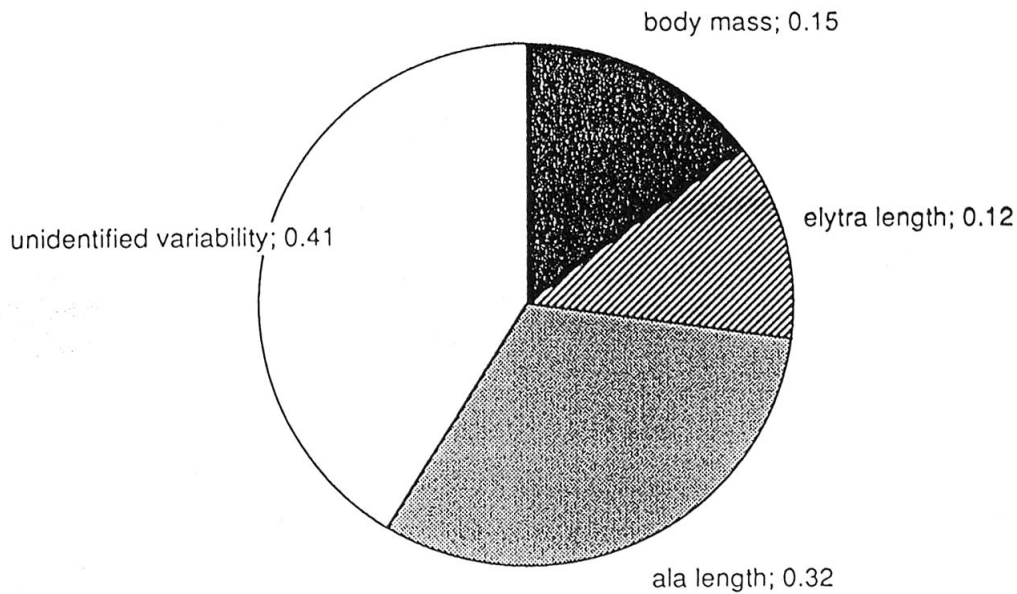


Fig. 6. Relative importance of body mass, elytra length and ala length in predicting wing beat frequency. Values indicate standard partial regression coefficients as a fraction of the amount of variability they explain.

beat frequency was proportional to wing length to the power of -1.28 , a value, which due to the large scatter in the data (compare fig. 7), was not significantly different from -1 . Wing length was proportional to mass to the power of 0.25 , significantly ($p \leq 0.05$) departing from 0.33 . In Diptera, finally, wing beat frequency scaled with wing length $^{-0.55}$ and wing length was proportional to mass to the power of 0.22 , again significantly different from 0.33 .

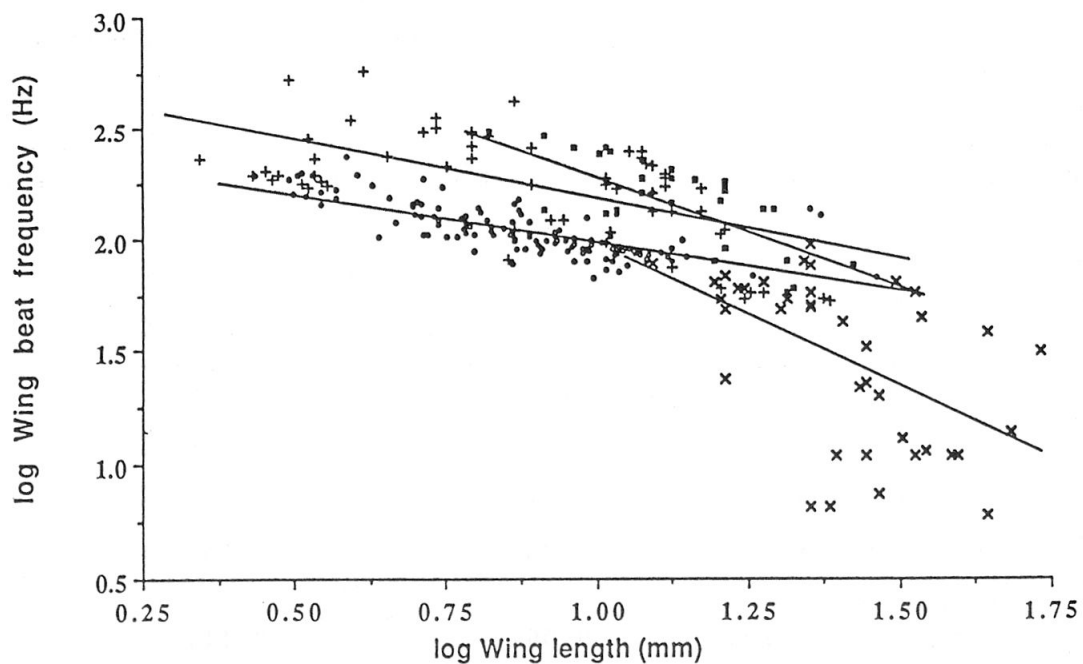


Fig. 7. Relationship of wing beat frequency and wing length in four insect orders. Hymenoptera, Diptera, and Lepidoptera data are from GREENEWALT (1962).

DISCUSSION

Morphometrics and frequency in beetles

The data are discussed based on similarity criteria given by ALEXANDER (1982) and a distinction among geometrical, elastic, and dynamic similarity is made. Theories of geometrical similarity imply that all linear dimensions (l) should be proportional to body mass^{1/3} (m) and all areas to body mass^{2/3} (ALEXANDER, 1982). By contrast, elastic similarity is based on the premise that terrestrial animals have homologous parts made of equal density and equal elastic moduli, and should be scaled in such a way as to deform under gravity in a geometrically similar fashion. Under these criteria wing length is proportional to body mass to the power of $1/4$. Dynamic similarity occurs if motions can be made identical by uniform changes of the scales in length and time. Dynamic similarity is said to occur if motions have similar Froude numbers v^2/gl , where v is a speed, and g the acceleration caused by gravity (DUNCAN, 1953).

According to these criteria, body mass, body length, ala length, and ala area are geometrically similar within the order Coleoptera. Correspondingly, wing loading increased with size in proportion to mass^{1/3}, as would be predicted from geometric similarity (LIGHTHILL, 1977). Only elytron lengths deviated from geometrical similarity; larger beetles had relatively larger elytra than did smaller species. Other types of similarity did not occur in beetles. Such virtually perfect geometric similarity is rare among insects, and in most cases the exponents of the allometric equations of morphological parameters on body mass are higher than predicted based on geometric similarity (see ALEXANDER, 1982), although a reanalysis of GREENEWALT's (1962) data arranged by orders indicated lower values than predicted.

The strong correlation of wing beat frequency with morphometric parameters is a well accepted fact. Due to the work of SOTAVALTA (1947), a large data set is available, which prompted several researchers to propose theories explaining, in particular, the relationship between n and wing length. GREENEWALT (1960) suggested that n of flying animals is equal to the fundamental frequency of a mechanical oscillator of similar dimensions and elastic properties. Later he (GREENEWALT, 1962) subdivided insects into groups with geometrically similar wing areas, and found that in each of these groups wing beat frequency scaled with approximately the -1.0 power of wing length, the slope that is predicted based on his mechanical theory. LIGHTHILL (1977) continued by identifying factors tending to limit the range of feasible frequencies for given linear dimensions in geometrically similar animals. WEIS-FOGH (1977) distinguished between intra and interspecific comparisons, and formulated a general interspecific rule in which $n \propto l^{-1}$. His interspecific rule was supported in several well defined insect groups such as Apoidea, Vespoidea, Noctuidea, Sphingidae, and Culicidae or in insect orders, such as Lepidoptera and Hymenoptera.

In beetles wing beat frequency scaled with length to the power of $-1/2$, a relationship quite different from that proposed by GREENEWALT (1962) and WEIS-FOGH (1977), although still within the range indicated by LIGHTHILL (1977). Why do beetles differ from the relationships proposed by GREENEWALT and WEIS-FOGH? Explanations suggested for other taxa, also deviating from $n \propto l^{-1}$, include lack of geometric similarity and confounding effects of wing loading. MAY (1981) accounted for $n \propto l^{-0.47}$ in dragonflies with lack of geometric similarity of the wings. In beetles, however, the alae are strictly geometrically similar and only a

slight deviation from geometrical similarity occurs in the elytra. The small deviation found in the elytra is not an issue in this regard, since elytra allometry should increase the exponent rather than increase it. MAY (1981) further showed that much of the variation in n can be explained by wing loading, and that in groups with constant wing loadings, n varied with wing length with exponents closer to the predicted value of -1 , than if groups with different wing loadings were compared. In beetles, however, analyses of species with similar wing loadings did not yield exponents different from -0.5 . For example $n \propto l^{-0.58}$ for all species with a wing loading of $0.5 (\pm 0.05) \text{ mg/mm}^2$ ($n = 20$).

The situation in beetles can be explained if, in addition to geometric similarity, an equal mass-specific force driving wing beat frequency is assumed over the entire size range. If this is done, scaling predictions parallel those found in beetles (see ECONOMOS, 1982): In geometrically similar animals Newton's second principle postulates the constancy of the acceleration of gravity (g) for all mechanically similar objects and because $g \propto l/T^2$, the assumption $g = \text{constant}$, leads to $t \propto l^{1/2}$ or $n \propto l^{-1/2}$, where t is time. Newton's principle can be extended to forces other than gravity, if an equal mass-specific force is applied. In other words, $n \propto l^{-1/2}$ implies that flying beetles drive their wing beat frequencies with the same wing mass specific force. This extension is only applicable if beetles have equal wing beat amplitudes, an assumption not investigated to date. The scaling of wing mass specific forces with other morphological parameters such as muscle cross section, depends on the scaling of wing mass with these parameters and on the scaling of force transmission efficiency, two factors requiring further investigation. The conclusion of equal mass specific forces is akin to Lighthill's (1977) constraint of equal lift coefficients if $n \propto l^{-1/2}$. The line of argumentation is different, but uses the same basic physical principles. The idea is further reiterated by WEIS-FOGH (1977) in his "aerodynamic rule".

A system of scaling in which mass specific power requirements and lift coefficients are constant over a large mass range implies that the wings are mounted elastically, beat at their natural frequency and consequently the inertial power requirement is eliminated (ALEXANDER, 1982).

Several other lines of evidence suggest beetles flap their wings at frequencies set by resonant properties of the thorax: Beetles possess asynchronous muscles in which the frequency of contraction is not determined by the output pattern of the nervous system (PRINGLE, 1967, 1978). Circumstantial evidence in this respect 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 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).

Large inertial power requirements are not possible in a system of geometric scaling because the specific bending moments for aerodynamic and inertial forces increase proportionally to wing length, and because the inertial moment is balanced against the elastic moment for only one body mass (WEIS-FOGH, 1977). Beetles without the optimum match would be at a disadvantage. Furthermore, the elimination, or at least reduction of inertial power requirements has the obvious benefit of increasing flight efficiency, a trait likely to be favored by selection.

The scaling of wing area (A) with n can be directly derived from the relationship between wing length with frequency. Because $n \propto l^{-1/2}$ and $l \propto A^{-1/2}$ it

follows that $n \propto A^{-1/4}$. The same holds true for body mass (m). Because $n \propto l^{-1/2}$ and $l \propto m^{1/3}$ it follows that $n \propto m^{-1/6}$, a value not significantly different from the observed $m^{-0.13}$. Body length, on the other hand, does not directly affect aerodynamic lift, and therefore beetles can afford more variability in this parameter, probably explaining why n is not proportional to body length $^{-1/2}$, even though wing length is proportional to body length.

Comparison with other insect orders

In his analysis, GREENEWALT (1962) arbitrarily divided the insects into geometrically similar groups, however did not consider taxonomic affinity. If the same data are ordered taxonomically, and if confounding intraspecific variation is eliminated by calculating species averages, a somewhat different picture from that of GREENEWALT emerges: while both Lepidoptera and Hymenoptera scale with $n \propto l^{-1}$, this is not the case in Diptera, in which, similar to Coleoptera, $n \propto l^{-1/2}$. In terms of geometric similarity, only in the order Coleoptera does wing length scale with mass to the power of 0.33; wing lengths are not geometrically similar in Hymenoptera, Lepidoptera, Diptera or as MAY (1981) indicated, in Odonata. Among orders the beetles therefore present an exception in their uniformity. The different situations occurring in other orders indicate the importance of different constraints on wing beat frequency. Even though beetles are the only geometrically similar insect order, precisely in this group frequency was not proportional to wing length to the power of -1 , as predicted by GREENEWALT (1962) and WEIS-FOGH (1977). However, further work is necessary before $n \propto l^{-1/2}$ can be postulated for geometrically similar animals on the ordinal level.

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ZUSAMMENFASSUNG

In 126 Käferspezies (Coleoptera) wurden die durchschnittlichen Flügelschlagfrequenzen (n) während freiem Flug, die Körpermassen und -längen, die Elytren- und Alalängen sowie die Alalflächen bestimmt. Der Grössenbereich der Körpermassen umfasste vier Zehnerpotenzen. Die meisten morphologischen Parameter wiesen signifikante Korrelationen mit n auf. Mit der Ausnahme der Elytrenlänge waren alle morphologischen Parameter untereinander geometrisch ähnlich. Die Flügelschlagfrequenz war proportional zu Alalänge $^{-1/2}$ ($n \propto l^{-1/2}$), ein Verhältnis, welches signifikant von den harmonischen Oszillatormodellen von GREENEWALT (1960) und WEIS-FOGH (1977) abweicht, wonach $n \propto l^{-1}$ sein soll. Ein Vergleich mit anderen Insektenordnungen zeigte, dass geometrische Ähnlichkeit eine Eigenheit der Käfer ist.

Aufgrund des 2. Hauptsatzes von Newton wird durch $n \propto l^{-1/2}$ impliziert, dass Käfer in allen Grössenordnungen die gleiche massenspezifische Kraft aufwenden, um ihre Flügel zu bewegen. Weiter kann aus $n \propto l^{-1/2}$ geschlossen werden, dass ein grosser Teil der kinetischen Energie am Ende eines Flügelschlages in Form von elastischer Energie erhalten bleibt.

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