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Relationship between morphometrics and wing beat frequency (intraspecific scaling) in five species of beetles (Coleoptera)

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In five beetle species (*Popillia japonica* Scarabaeidae, *Coleomegilla fuscilabris* Coccinellidae, *Epicauta pennsylvanica* Meloidae, *Chauliognathus pennsylvanicus* Cantharidae, *Photinus pyralis* Lampyridae) intraspecific variation in wing beat frequency *(n)*, and body and wing morphology were measured. With the exception of *Chauliognathus* the scaling exponents of linear dimensions (l) (e. g. body, elytron, ala length) with body mass (m) were not significantly different from that of elastic similarity, i. e. $l \alpha m^{1/4}$. In two species *(Popillia, Photinus)* ala areas (A) were also elastically similar, while in the other two species *(Coleomegilla, Epicauta)* scaling exponents were considerably smaller than $A \alpha m^{1/2}$. In contrast to geometrical similarity found interspecifically in the order, elastic similarity reduces the variation of wing beat frequency over a given size range. Instead of $n \alpha m^{-1/6}$, as would be expected under conditions of geometric similarity, $n \alpha m^{-1/8}$, even though $n \alpha l^{-1/2}$ in both cases. The tendency to reduce variation in wing beat frequency over given mass ranges is enhanced in *Coleomegilla* and *Epicauta* as a result of the scaling exponents for frequency and ala area which were smaller than predicted by elastic or geometric similarity.

Calculation of partial regression coefficients of various morphometric characters determining wing beat frequency showed that a) morphometric parameters explain different amounts of the variability in wing beat frequency in different species, and b) different morphological parameters differ in their relative importance in different species.

INTRODUCTION

Traditionally, comparative physiologists have analyzed differences among species and described the functional response of the average animal of the group (BENNET, 1987). Although useful, this approach neglects the inherent high variability among biological organisms. In contrast to the average of a species a real individual is a unique combination of traits, and should therefore provide useful insight.

This study addresses intraspecific scaling of wing beat frequency *(n)* with body and wing morphology in five species of beetles. Wing beat frequency is an important component of aerodynamic lift production and is therefore closely tied to the energetic requirements of flight (CASEY, 1989).

Morphological constraints imposed on wing beat frequency vary in different taxa, which led WEIS-FOGH (1977) to describe "rules" of how wing beat frequency scales in relation to wing length. Similarily LIGHTHILL (1977) proposed limiting conditions based on various morphological and aerodynamic constraints, within which wing beat frequency might vary with linear dimensions (l).

Several authors have studied the scaling of wing beat frequency and morphology on an interspecific basis (GREENEWALT, 1962; MAY, 1981). However few data are available on the variation of morphology and wing beat frequency for an individual species. WEIS-FOGH (1977) listed reasons, mainly based on

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the relatively modest variation in size found within members of a given species, why intraspecific scaling might be different from interspecific scaling. This distinction led him to formulate the intraspecific rule, in which $n \propto l^{-2/3}$, in contrast to his interspecific rule, in which $n \propto l^{-1}$. The scaling of wing beat frequency and wing length within *Schistocerca gregaria* (WEIS-FOGH, 1956; SOTAVALTA, 1947) closely followed this rule, but verification in other taxa is lacking and different scaling mechanisms, reflecting adaptations to specific situations are possible.

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 between organisms. 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 within a given beetle species.

The current study further discusses the relative importance of various morphometric characters in determining wing beat frequency. Because beetles possess myogenic muscles (PRINGLE, 1967, 1978) it is generally assumed that the resonance properties of the flight system determine wing beat frequency. Wing and body morphology are important components thereof, and corresponding interspecific studies abound (review: CASEY, 1989), although intraspecific data are lacking.

MATERIALS AND METHODS

The following five species were considered: *Popillia japonica* NEWMAN (Scarabaeidae), *Coleomegilla fuscilabris* MULSANT (Coccinellidae), *Epicauta pennsylvanica* DE GEER (Meloidae), *Chauliognathus pennsylvanicus* DE GEER (Cantharidae), and *Photinus pyralis* L. (Lampyridae). All species were measured in the vicinity of New Brunswick, N.J., USA 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 beetles could not readily be observed to fly in the field, they were captured with a net and subsequently placed in a small box open on top, which in turn was placed in a larger, transparent plastic container. In most cases the beetles would climb to the top of the smaller container and then take off, usually heading towards the rim of the larger container. During this period of free flight wing beat frequency could be measured. All beetles were measured within 15 minutes of capture and were not allowed to fly during this period of time.

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.). Then ala loading and ala aspect ratio could be calculated (ELLINGTON, 1984).

The current data set is an extension of data used to determine the effects of thoracic and ambient temperature on wing beat frequency, so all measurements were undertaken over a range of temperatures. See OERTLI (1989) for a discussion of temperature effects on frequency.

RESULTS

Average wing beat frequencies, body size, and wing shape parameters as well as standard errors and ranges are listed in Tab. 1. In all species the body mass of the largest individual was at least twice that of the smallest.

In most cases strong correlations between other morphological features and body mass occurred (Tab. 2). An exception was *Chauliognathus pennsylvanicus* in which only a comparatively small and often non-significant portion of the variability in morphology could be explained by variability in body mass. The scaling of morphology and mass varied between species and corresponding allometric equations are given in Tab. 2. Wing beat frequency also correlated significantly with most morphological characters and corresponding allometric equations are given in Tab. 3.

In an effort to determine the relative importance of the different morphological parameters in explaining variation in wing beat frequency, standard partial regression coefficients were calculated. Because all morphological size parameters were correlated with one another, not all assumptions for calculating multiple regression coefficients (slopes) are fulfilled. However, the principle problem of multicolinearity is an increase in the standard errors of the regression coefficients while the coefficients themselves remain unbiased, allowing calculation of similarly unbiased standard partial regression coefficients (see STEELE & TORRIE, 1960). Tab. 4 gives the multiple regression equations for which over all species the largest amount of variability in wing beat frequency could be explained, and the standard partial regression coefficients for these parameters are shown in Tab. 5. The parameters included are thoracic temperature, body mass, elytron length, ala length, and ala aspect ratio. Although the influence of thoracic temperature on n is the focus of another study (OERTLI, 1989), it is included in the multiple regressions in order to facilitate comparison. Three observations are noteworthy in respect to partial regression coefficients: 1) morphometric parameters explain a different amount of the variation in wing beat frequency in different species, 2) the different morphological parameters differ in their relative importance in different species, and 3) in some species aspect ratio is an important determinant of frequency, despite the lack of correlation with frequency on an interspecific basis.

DISCUSSION

Intraspecific Scaling

A generale rule applying to the intraspecific scaling of all five species is not immediately obvious and therefore the situation is first analyzed separately by species. The data are discussed based on the similarity criteria given in ALEXANDER (1982) and a distinction among geometrical, elastic, and dynamic similarity is made. These types of similarity, and theoretical predictions based on these similarity criteria of how frequency might scale with morphology and body mass are hypothesis testable with the current data set. First, these theories and their predictions are described:

Geometrical similarity implies that all linear dimensions (l) should be proportional to body mass (m)$^{1/3}$, and all areas (A) to m$^{2/3}$. If geometric similarity occurs, a prediction of the scaling of wing beat frequency can be made if an equal mass specific force driving wing beat frequency is assumed over the entire size

Tab. 1. Averages, standard deviations, and range of wing beat frequency and morphological parameters. Since ala aspect ratio and ala loading are values calculated from other parameters, standard deviations for these two are not given.

Parameter	Average	Standard Deviation	Range
Popillia japonica (n=100)			
Frequency (Hz)	118.5	8.94	100 - 137
Body mass (mg)	93.2	19.99	63 - 136
Body length (mm)	10.0	0.73	70 - 146
Elytron length (mm)	5.96	0.34	5.3 - 6.8
Ala length (mm)	10.45	0.58	9.2 - 12.1
Ala area (mm^2)	58.6	5.12	45 - 78
Ala aspect ratio	3.73		3.05 - 4.51
Ala loading (mg/mm^2)	0.80		0.61 - 0.95
Coleomegilla fuscilabris (n=61)			
Frequency (Hz)	95.2	10.8	84 - 118
Body mass (mg)	12.2	2.96	4.1 - 18.3
Body length (mm)	5.67	0.45	3.8 - 6.3
Elytron length (mm)	4.79	0.32	3.8 - 6.0
Ala length (mm)	6.56	0.38	6.0 - 8.0
Ala area (mm^2)	18.8	2.46	15.2 - 22.6
Ala aspect ratio	4.58		3.3 - 5.8
Ala loading (mg/mm^2)	0.32		0.23 - 0.48
Epicauta pennsylvanica (n=51)			
Frequency (Hz)	99.1	6.93	82 - 102
Body mass (mg)	55.2	9.47	24 - 103
Body length (mm)	9.47	2.36	8.5 - 11.3
Elytron length (mm)	8.14	0.65	7.4 - 10.0
Ala length (mm)	9.91	0.73	8.3 - 11.4
Ala area (mm^2)	60.4	5.12	31 - 75
Ala aspect ratio	3.25		2.9 - 3.9
Ala loading (mg/mm^2)	0.46		0.31 - 1.05
Chauliognathus pennsylvanicus (n=102)			
Frequency (Hz)	88.7	5.75	73 - 101
Body mass (mg)	38.4	15.0	11 - 68
Body length (mm)	10.52	0.91	9.4 -13.0
Elytron length (mm)	7.73	0.43	7.2 - 9.1
Ala length (mm)	9.47	0.52	8.2 - 10.5
Ala area (mm^2)	56.9	5.78	34 - 61
Ala aspect ratio	3.15		2.1 - 5.2
Ala loading (mg/mm^2)	0.34		0.19 - 1.01
Photinus pyralis (n=75)			
Frequency (Hz)	60.8	4.88	51 - 73
Body mass (mg)	25.9	8.96	5 - 48
Body length (mm)	11.3	0.91	9.5 - 12.8
Elytron length (mm)	9.51	0.72	7.0 - 9.7
Ala length (mm)	9.56	0.71	7.1 - 10.2
Ala area (mm^2)	58.2	6.24	24 - 72
Ala aspect ratio	3.14		2.1 - 3.7
Ala loading (mg/mm^2)	0.22		0.16 - 0.43

Tab. 2. Regression equations for morphology as a function of body mass. Based on $\log_{10}$ transformed data.

Parameter	r^2	Slope	y-intercept
Popillia japonica n=100; $r^2>0.038$			
Body length (mm)	0.716	0.266±0.039	0.506±0.077
Elytron length (mm)	0.425	0.222±0.042	0.331±0.082
Ala length (mm)	0.548	0.233±0.034	0.562±0.067
Ala area (mm^2)	0.433	0.392±0.080	0.993±0.156
Ala loading (mg/mm^2)	0.593	0.608±0.080	-0.993±0.156
Ala aspect ratio	0.056	0.042±0.063	0.785±0.124
Coleomegilla fuscilabris n=61; $r^2>0.063$			
Body length (mm)	0.151	0.286±0.098	0.391±0.107
Elytron length (mm)	0.518	0.374±0.074	0.270±0.081
Ala length (mm)	0.295	0.328±0.104	0.493±0.114
Ala area (mm^2)	0.076	0.191±0.089	1.070±0.115
Ala loading (mg/mm^2)	0.598	0.809±0.105	-1.070±0.115
Ala aspect ratio	0.058	0.265±0.238	0.693±0.259
Epicauta pennsylvanica n=51; $r^2>0.075$			
Body length (mm)	0.650	0.253±0.047	0.574±0.022
Elytron length (mm)	0.759	0.261±0.027	0.471±0.046
Ala length (mm)	0.570	0.224±0.036	0.606±0.061
Ala area (mm^2)	0.085	0.259±0.212	1.326±0.355
Ala loading (mg/mm^2)	0.434	0.741±0.212	-1.326±0.355
Ala aspect ratio	0.137	0.263±0.165	0.403±0.277
Chauliognathus pennsylvanicus n=102; $r^2>0.038$			
Body length (mm)	0.021	0.031±0.033	0.973±0.050
Elytron length (mm)	0.147	0.062±0.023	0.818±0.037
Ala length (mm)	0.063	0.040±0.024	0.897±0.039
Ala area (mm^2)	0.029	0.047±0.048	1.596±0.075
Ala loading (mg/mm^2)	0.925	0.953±0.048	1.596±0.074
Ala aspect ratio	0.263	-0.119±0.076	1.076±0.114
Photinus pyralis n=75; $r^2>0.051$			
Body length (mm)	0.508	0.239±0.050	0.713±0.072
Elytra length (mm)	0.691	0.309±0.044	0.489±0.063
Ala length (mm)	0.706	0.303±0.042	0.500±0.060
Ala area (mm^2)	0.188	0.396±0.175	1.184±0.251
Ala loading (mg/mm^2)	0.350	0.604±0.175	-1.184±0.250
Ala aspect ratio	0.567	0.408±0.116	0.118±0.172

range (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 $g \alpha 1/t^2$, the assumption g = constant, leads to $t \alpha l^{1/2}$ or $n \alpha l^{-1/2}$ and correspondingly $n \alpha m^{-1/6}$, where t is time. Newton's principle can be extended to other forces, if an equal mass-specific force is applied.

Tab. 3. Regression equations for wing beat frequency as a function of body and wing morphology. Based on $\log_{10}$ transformed data. Regressions are significant if values are above indicated r^2.

Parameter	r^2	Slope	y-intercept
Popillia japonica n=100; r^2>0.038			
Body mass (mg)	0.288	-0.180±0.034	2.420±0.067
Body length (mm)	0.309	-0.558±0.209	2.628±0.216
Elytron length (mm)	0.388	-0.640±0.130	2.558±0.100
Ala length (mm)	0.192	-0.492±0.162	2.568±0.165
Ala area (mm^2)	0.118	-0.187±0.096	2.394±0.169
Ala loading (mg/mm^2)	0.191	-0.191±0.072	2.103±0.015
Ala aspect ratio	0.046	-0.207±0.176	2.245±0.153
Coleomegilla fuscilabris n=61; r^2>0.063			
Body mass (mg)	0.040	-0.069±0.057	2.050±0.061
Body length (mm)	0.139	-0.348±0.134	2.216±0.094
Elytron length (mm)	0.041	-0.320±0.339	2.174±0.229
Ala length (mm)	0.040	-0.290±0.310	2.205±0.264
Ala area (mm^2)	0 049	-0.299±0.166	2.266±0.212
Ala loading (mg/mm^2)	0.012	-0.076±0.115	1.960±0.024
Ala aspect ratio	0.097	-0.289±0.208	2.242±0.205
Epicauta pennsylvanica n=51; r^2>0.075			
Body mass (mg)	0.026	-0.035±0.030	2.003±0.052
Body length (mm)	0.071	-0.238±0.223	2.192±0.033
Elytron length (mm)	0.043	-0.151±0.129	2.087±0.118
Ala length (mm)	0.071	-0.193±0.128	2.140±0.127
Ala area (mm^2)	0.329	-0.188±0.067	2.286±0.118
Ala loading (mg/mm^2)	0.073	0.070±0.062	1.961±0.009
Ala aspect ratio	0.050	0.091±0.100	1.878±0.084
Chauliognathus pennsylvanicus n=102; r^2>0.038			
Body mass (mg)	0.051	0.038±0.016	1.888±0.025
Body length (mm)	0.041	-0.180±0.134	2.127±0.137
Elytron length (mm)	0.002	-0.058±0.166	2.001±0.152
Ala length (mm)	0.099	-0.336±0.158	2.271±0.152
Ala area (mm^2)	0.016	-0.087±0.199	2.058±0.163
Ala loading (mg/mm^2)	0.160	0.075±0.030	1.928±0.008
Ala aspect ratio	0.012	0.051±0.172	1.860±0.206
Photinus pyralis n=75; r^2>0.051			
Body mass (mg)	0.056	-0.052±0.026	1.856±0.036
Body length (mm)	0.505	-0.601±0.127	2.406±0.134
Elytron length (mm)	0.531	-0.570±0.114	2.301±0.106
Ala length (mm)	0.445	-0.539±0.128	2.273±0.120
Ala area (mm^2)	0.311	-0.178±0.057	2.082±0.087
Ala loading (mg/mm^2)	0.008	0.027±0.064	1.771±0.007
Ala aspect ratio	0.036	0.111±0.191	1.645±0.189

By contrast *elastic similarity* is based on the proposition that terrestrial animals have homologous parts made of materials of equal density and equal elastic moduli, and should be scaled in such a way as to deform under gravity in a geomet-

Tab. 4. Multiple regression equations of frequency as a function of morphology and thoracic temperature. With the exception of temperature, all data was $\log_{10}$ transformed.

Parameter	Regression Coefficient	Standard Error	Significance Level
Popillia japonica n=100; r^2=0.550			
Constant	2.219	0.204	0.000
Thoracic temperature (°C)	0.009	0.003	0.007
Body mass (mg)	-0.020	0.073	0.789
Elytron length (mm)	-0.456	0.193	0.025
Ala length (mm)	-0.099	0.255	0.700
Ala aspect ratio	0.017	0.143	0.906
Coleomegilla fuscilabris n=61; r^2=0.286			
Constant	2.236	0.587	0.001
Thoracic temperature (°C)	-0.008	0.014	0.567
Body mass (mg)	-0.247	0.339	0.477
Elytron length (mm)	-0.296	1.050	0.781
Ala length (mm)	1.910	1.268	0.149
Ala aspect ratio	-1.194	0.546	0.042
Epicauta pennsylvanica n=51; r^2=0.670			
Constant	1.938	0.178	0.000
Thoracic temperature (°C)	0.007	0.003	0.037
Body mass (mg)	0.005	0.083	0.948
Elytron length (mm)	0.594	0.241	0.025
Ala length (mm)	-0.937	0.232	0.001
Ala aspect ratio	0.188	0.077	0.026
Chauliognathus pennsylvanicus n=102; r^2=0.661			
Constant	2.097	0.509	0.004
Thoracic temperature (°C)	0.006	0.007	0.444
Body mass (mg)	-0.001	0.098	0.993
Elytron length (mm)	0.144	1.359	0.918
Ala length (mm)	-0.660	1.426	0.657
Ala aspect ratio	0.214	0.418	0.624
Photinus pyralis n=75; r^2=0.943			
Constant	2.199	0.192	0.000
Thoracic temperature (°C)	0.008	0.006	0.209
Body mass (mg)	0.146	0.071	0.071
Elytron length (mm)	-0.585	0.299	0.082
Ala length (mm)	-0.549	0.334	0.134
Ala aspect ratio	0.280	0.103	0.024

rically similar fashion. Under these criteria l is proportional to body mass to the power of 1/4. Since two dimensional properties are composed of two linear dimensions ($l \propto A^{1/2}$) elastic similarity implies $A \propto m^{1/2}$. Here again frequencies are predictable if one assumes that frequency is proportional to the natural frequency of the wing. The resonant frequency is proportional to $(\text{stiffness}/\text{mass})^{1/2}$ which is, by definition of elastic similarity, proportional to $l^{-1/2}$, $A^{-1/4}$, or $m^{-1/8}$. The scaling of frequency and length are therefore identical in both elastic and geometrical similarity, but the scaling of mass and frequency differ.

Tab. 5. Standard partial regression coefficients based on multiple regression equations listed in Tab. 4. With the exception of temperature, all data was $\log_{10}$ transformed.

Parameter	Regression Coefficient
Popillia japonica n=100; r^2=0.550	
Thoracic temperature (°C)	0.516
Body mass (mg)	0.055
Elytron length (mm)	0.441
Ala length (mm)	0.087
Ala aspect ratio	0.016
Coleomegilla fuscilabris n=61; r^2=0.286	
Thoracic temperature (°C)	0.304
Body mass (mg)	0.598
Elytron length (mm)	0.211
Ala length (mm)	1.579
Ala aspect ratio	1.654
Epicauta pennsylvanica n=51; r^2=0.670	
Thoracic temperature (°C)	0.809
Body mass (mg)	0.023
Elytron length (mm)	1.034
Ala length (mm)	1.378
Ala aspect ratio	0.453
Chauliognathus pennsylvanicus n=102; r^2=0.661	
Thoracic temperature (°C)	0.866
Body mass (mg)	0.006
Elytron length (mm)	0.132
Ala length (mm)	0.634
Ala aspect ratio	1.641
Photinus pyralis n=75; r^2=0.943	
Thoracic temperature (°C)	0.664
Body mass (mg)	0.725
Elytron length (mm)	0.687
Ala length (mm)	0.629
Ala aspect ratio	0.486

Dynamic similarity, finally, 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 the same Froude numbers v^2/gl, where v is a speed, and g the acceleration caused by gravity (DUNCAN, 1953). The characteristic speed used in the present analysis is the speed of the wing tip, calculated from frequency and wing length, under the assumption that all individuals of a given species are operating at the same amplitudes. Under these conditions, similar Froude numbers over a range of frequencies can only occur if frequency is not correlated to ala length, i. e. $n \propto l^0$. This relationship can be used as a criterion for dynamic similarity. Some care must be applied to the assumption that all individuals of a given species operate at the same amplitude. In Japanese beetles *(P. japonica)* a standard deviation of

22.01 (average 152.3 degrees) and in soldier beetles *(C. pennsylvanicus)* a standard deviation of 25.3 (average 140.2) were found in intraspecific comparisons of wing beat amplitudes (Oertli & Oertli, 1990).

How do the data compare with the above theories and predictions?

Popillia japonica

In the Japanese beetle, geometrical similarity of wing lengths and areas did not occur; allometric exponents differed significantly from $l \alpha m^{1/3}$ and $A \alpha m^{2/3}$. Likewise, dynamic similarity did not occur because wing beat frequency and ala length were significantly correlated with one another. By constrast, no significant deviations from predictions based on elastic similarity, either for morphology and wing beat frequency, occurred. *Popillia* therefore seems to be a prime example of elastic similarity.

Coleomegilla fuscilabris

Wing beat frequency and ala length were significantly correlated with one another, and therefore dynamic similarity did not apply. Due to the large standard errors found in this species, neither elastic or geometric similarity can be rejected for linear dimensions. By contrast, both types of similarity must be rejected for wing areas: individuals with larger body masses had smaller wing areas (both elytra and alae) than would be predicted from either type of similarity. Consequently ala loading increased dramatically with size. Because ala length increased either geometrically or elastically and wing area did not, aspect ratio increased with increases in body mass. Correspondingly, wing beat frequency scaled with ala length and body mass with exponents smaller than predicted from either type of similarity. In other words, the lack of geometric or elastic similarity in ala area reduces the variation in wing beat frequency over a given mass range.

Epicauta pennsylvanica

In the black blister beetle neither geometric nor dynamic similarity occurred. With the exception of ala area, the exponents fit predictions based on elastic similarity. The exponents for ala area were smaller than predicted for elastic similarity. The situation is similar to that of *Coleomegilla fuscilabris* and correspondingly wing beat frequency scales with ala length and body mass with exponents smaller than predicated based on elastic similarity, reducing, in effect, the variation of wing beat frequency over a given mass range.

Chauliognathus pennsylvanicus

In the soldier beetle all three similarity criteria must be rejected. This is a result of the lack of correlation between morphological parameters and body mass. Differences in gravidity (pers. obs.), i. e. modification in body mass not affecting other parameters, is a likely reason for this lack of correlation. Consequently, no meaningful interpretation of the scaling of *n* and body mass is possible in this species. Wing beat frequency, however, was correlated with most morphological parameters, and in this respect soldier beetles are no different from the other species.

Photinus pyralis

In the lightning beetle, both geometric and dynamic similarity could be rejected. Predictions based on elastic similarity were not significantly different from the obtained data, both for linear dimensions and for ala area. The correlation of ala aspect ratio with body mass is a result of the tendency toward larger exponents, with which wing length scaled with mass, the smaller ones for wing area. This variation in aspect ratio however did not correlate with wing beat frequency, and predictions concerning the wing beat frequency of elastically similar objects are essentially fulfilled.

Conclusion

With the exception of *Chauliognathus pennsylvanicus,* in which such an interpretation is all but impossible, linear size differences within beetle species seem to be characterized by elastic similarity. This contrasts to the geometric similarity found in interspecific comparisons in the order (Oertli, 1991). Why this difference? Elastic similarity is based on the premise that animals have parts of equal density and equal elastic moduli. This proposition is more likely within a given species than among different species.

Interspecifically, by contrast, structural differences may occur in order to allow geometrical similarity. Due to the large body mass range found interspecifically, geometric similarity is probably of selective advantage by preventing overly large or small wings at the extreme ends of the mass range. Intraspecifically, the range of body masses is much smaller, and therefore other constraints become more important, such as deformation under gravity as found in elastic similarity.

Another intriguing possibility of why elastic and not geometric similarity occurs intraspecifically considers the consequences on wing beat frequency. Predictions concerning the scaling of wing beat frequency and linear dimensions are identical for both elastic and geometric similarity while frequency variation is smaller over a given range of body masses if shapes are elastically similar. This fact may explain why elastic and not geometric similarity occurs. This tendency to reduce variation in wing beat frequency over a size range is enhanced by the lack of elastic of geometric similarity in wing area in three species. Reasons therefore seem elusive. Energetic constraints are unlikely, since wing beat frequency and rates of oxygen consumption were not correlated in either soldier or Japanese beetles (Oertli & Oertli, 1990). Since wing beat frequency was shown to influence flight agility (J. J. Oertli, in preparation), it is possible that selection favored individuals of a certain flight agility in a given species. Further investigation of beetle flight are necessary to test this hypothesis and to elucidate selective forces responsible for the tendency to equalize wing beat frequency over a range of body sizes within a species.

Few data are available for comparison with other orders. In the sphingid moth *Hyles lineata* wing length scaled with mass to the power of 0.38 and wing area was proportional to mass to the power of 0.68 (Casey, 1976). Both values approximate values based on geometric similarity. In *Manduca sexta,* the corresponding values were 0.26 and 0.56 respectively (Casey, 1976), approaching elastic similarity. In terms of frequency, Weis-Fogh (1956) found $n \alpha l^{-2/3}$ in *Schistocerca gregaria,* the same relationship found by Sotavalta (1956) in wing mutilation experiments. Although not extensive, these data do indicate potentially different situations in other taxa, possibly reflecting adaptation to specific situations.

Influence of morphology on frequency

Obviously no general rule describes the influence of morphometrics on wing beat frequency within a species. The morphometric parameters individually explained different portions of the variability in wing beat frequency, and in combination explained a different portion of the total variability among species. This indicates the importance of other elements. Temperature is one such factor (see OERTLI, 1989), but others, such as the elastic properties of the cuticle, muscle, and wing base may be important as well.

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ZUSAMMENFASSUNG

In fünf Käferarten *(Popillia japonica* Scarabaeidae, *Coleomegilla fuscilabris* Coccinellidae, *Epicauta pennsylvanica* Meloidae, *Chauliognathus pennsylvanicus* Cantharidae, *Photinus pyralis* Lampyridae) wurde die intraspezifische Variabilität zwischen Flügelschlagfrequenz *(n)* und Körper- und Flügelmorphologie gemessen. Mit Ausnahme von *Chauliognathus* wiesen lineare Dimensionen (l; z.B. Körper-, Elytrenlänge) eine elastische Ähnlichkeit zur Körpermasse (m) auf, d.h. l war proportional (α) zu $m^{1/4}$. Im Gegensatz zur geometrischen Ähnlichkeit, welche interspezifisch nachgewiesen werden konnte, reduziert elastische Ähnlichkeit die Variationsmöglichkeiten für Flügelschlagfrequenzen bei gegebenen Bandbreiten von Körpermassen. Anstelle von $n \alpha m^{-1/6}$ (geometrische Ähnlichkeit) ist $n \alpha m^{-1/8}$ (elastische Ähnlichkeit), obwohl $n \alpha l^{-1/2}$ in beiden Fällen. Die Tendenz, die Variationsmöglichkeiten bei der Flügelschlagfrequenz zu reduzieren, wird durch die kleinen Proportionalitätsfaktoren zwischen *n* und der Flügelfläche weiter verstärkt.

Die Berechnung partieller Regressionskoeffizienten verschiedener, die Flügelschlagfrequenz beeinflussender Faktoren zeigte, dass sowohl der Einfluss der Morphologie wie auch die relative Bedeutung verschiedener Parameter untereinander eine Funktion der untersuchten Spezies sind.

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