RELATIONSHIP BETWEEN WING LOADING, WINGBEAT FREQUENCY AND BODY MASS IN HOMOPTEROUS INSECTS

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SUMMARY

Several biophysical properties of members of Aleyrodidae and Aphididae were examined in order to explore how homopterous insects fly. Five species of aphids were found to weigh significantly more than five whitefly species (range $1\cdot14-7\cdot02\times10^{-4}$ g for aphids *vs* $3\cdot3-8\cdot0\times10^{-5}$ g for whiteflies) and to have significantly larger wing surface areas (range $0\cdot0103-0\cdot1106$ cm^2 *vs* $0\cdot0096-$ $0\cdot0264$ cm^2). As a consequence whiteflies and aphids can be partitioned into two groups with respect to wing loading (range $0\cdot00633-0\cdot01412$ g cm^{-2} for aphids, $1\cdot74-5\cdot23\times10^{-3}$ g cm^{-2} for whiteflies). Members of the two families are also separated in terms of wingbeat frequency (range $81\cdot1-123\cdot4$ Hz for aphids, $165\cdot6-224\cdot2$ Hz for whiteflies). Since our animals were much smaller than any insects examined previously for these parameters, values were compared with the same parameters for 149 insect species recorded in the literature. Using these data, we found wingbeat frequency to be significantly correlated with wing loading only in insects weighing more than $0\cdot03$ g. Larger insects seem to employ a strategy similar to other flying animals, by compensating for high wing loading with higher wingbeat frequencies. The lack of correlation for these two parameters in insects weighing less than $0\cdot03$ g probably results from the use of different flying strategies. These include employment of a clap and fling mechanism and the possession by some of exceedingly low wing loading. Also, small insects may have reduced settling velocities because they possess high drag coefficients. Previous studies which failed to establish a relationship between wing loading and wingbeat frequency in larger insects may have considered too few subjects or too great a range of body masses. The mass range is important because smaller insects which employ increased wingbeat frequency must use rates exponentially higher than those of larger insects utilizing the same strategy.

INTRODUCTION

Whiteflies do not as readily engage in vertical flight as other homopterous insects, such as aphids. This was discovered when Byrne, von Bretzel & Hoffman (1986)

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placed traps at heights of 0–15 cm, 50–65 cm and 100–115 cm to catch sweetpotato whiteflies, *Bemisia tabaci* (Gennadius) and bandedwinged whiteflies, *Trialeurodes abutilonea* (Haldeman). During two growing seasons, 81 % of the whiteflies were captured in the lowest traps, 12 % in the midlevel traps and 7 % in the highest traps. In a previous survey of alate aphids, Broadbent (1948) placed traps at heights of 5–36 cm, 81–118 cm and 157–188 cm. Over a 24-week period in his study, 14 % of the aphids were caught in the lowest traps, 34 % in the midlevel traps and 52 % in the highest traps. These findings led us to examine how members of these two homopterous families might differ in their flight mechanisms, particularly with regard to wing loading and wingbeat frequency.

MATERIALS AND METHODS

The members of Aleyrodidae we examined were *Aleurothrixus floccosus* (Maskell), *Bemisia tabaci, Dialeurodes citri* (Ashmead), *Trialeurodes abutilonea* and *Trialeurodes vaporariorum* (Westwood). Members of Aphididae were *Aphis fabae* Scopoli, *Aphis gossypii* Glover, *Aphis nerii* Fonscolombe, *Acyrthosiphon kondoi* Shinji and *Myzus persicae* (Sulzer). All species were reared in greenhouses or on research plots at agricultural experimental stations maintained by the University of Arizona at Tucson and the University of California at Riverside. Italian honeybees, *Apis mellifera* L., from the USDA Carl Hayden Bee Research Center in Tucson, AZ, were also measured to compare our data with those in the literature.

Using a Datamate 100 Microfiche Reader, we determined wing surface areas for all species by projecting images of their wings onto transparent acetate sheets. Templates of images were cut from the sheets and weighed. A linear regression equation, relating template masses of known dimensions to their surface areas, was developed. Surface areas for wings were calculated by inserting the masses of their templates into this equation. Wing lengths were determined using an ocular micrometer in a dissecting microscope. Fresh whole masses were obtained by immobilizing the insects with carbon dioxide and weighing them with either a Cahn 25 or Cahn 29 Microbalance.

Wing loadings for these insects were calculated in $g\,cm^{-2}$ by dividing mass by total wing surface area. Total wing surface area was determined by summing twice the mean of the forewing area with twice the mean of the hindwing area.

Wingbeat frequencies were obtained with an optical tachometer, in a manner similar to that of Unwin & Ellington (1979), and a Nicolet 206 digital oscilloscope. Insects were allowed to fly freely inside a covered greenhouse at $24 \pm 3\,°C$. A wingbeat frequency was obtained for the sexually dimorphic *D. citri* but, since separate values could not be determined for the two sexes, this species was not considered in statistical comparisons of wingbeat frequencies.

The number of animals measured for each variable was determined by examining coefficients of variation as data sets were accumulated. The data were tested for normality using the Shapiro–Wilk statistic (Shapiro & Wilk, 1965). If samples were normally distributed, a *t*-test or Student *F*-test was used to compare sample means.

Otherwise, Ansari–Bradley (Ansari & Bradley, 1960) and Mann–Whitney (Mann & Whitney, 1947) nonparametric tests for equality of dispersion were used. Statistical analysis was done using the RS/1 software system on a Digital Equipment Corporation Professional 350 microcomputer.

To compare aphids and whiteflies with other insects, we compiled data from the literature for 149 insect species with known values for wing loading, wingbeat frequency and wing surface area. Certain data were corrected to match our selected format for presentation. Only species with known values for all three variables were used.

RESULTS

Morphometrics for our homopterans appear in Table 1 as numbers 1–11. Table 1 also provides rankings of the animals measured in this study with respect to values in the literature for the same parameters. These are shown parenthetically in the columns for mass, wing area, wing loading and wingbeat frequency. For example, *B. tabaci* wingbeat frequency ranked as the 134th highest of 158 recorded frequencies.

The data for the honeybees we measured appear as number 54 in Table 1. Our results compare favourably with those reported earlier by Magnan (1934) and Sotavalta (1952) which are shown as numbers 49 and 50.

All wing area and wing length measurements had low coefficients of variation (c.v.), <15 %, indicating that 20 individuals would constitute an adequate sample size. Wingbeat frequencies also had low c.v. (<10 %), and only 10 individuals were measured. Body masses were more variable, and 40 individuals were weighed (c.v. <40 %). Unlike the other insects we measured, *D. citri* males and females were significantly different in terms of the two important flight-associated parameters: body mass and wing surface area ($P < 0.05$). Consequently, all values for the measured variables, with the exception of wingbeat frequency (not given), are listed separately for *D. citri* males and females.

Wing surface areas and lengths

The forewing surface areas of the measured animals were significantly larger than those of their hindwings ($P < 0.01$). Generally, aphids had significantly larger forewings and hindwings than whiteflies, although *Ap. gossypii* was an exception ($P < 0.01$). Aphid forewings and hindwings were also longer than the forewings and hindwings of whiteflies ($P < 0.01$) (Table 2).

Body masses

Body masses are given in Table 1. Aphids were significantly larger than whiteflies; ranges were $1.14–7.02 \times 10^{-4}$ g for aphids and $3.3–8.0 \times 10^{-5}$ g for whiteflies ($P < 0.01$). Almost all body masses of the measured animals were significantly different from one another ($P < 0.01$). The exceptions were two whiteflies, *D. citri* males and *T. vaporariorum* ($P > 0.01$).

Table 1. *Insect flight-associated morphometrics*

Family	Species	Mass (g)	Wing area (cm^2)	Wing loading (g cm^{-2})	Wingbeat frequency (Hz)	Citation
1. Aleyrodidae	*Bemisia tabaci*	3.3×10^{-5} (1)*	0.0134 (3)	2.45×10^{-3} (3)	168.6 (134)	Present study
2. Aleyrodidae	*Trialeurodes vaporariorum*	3.5×10^{-5} (2)	0.0165 (4)	2.12×10^{-3} (2)	180.0 (139)	Present study
3. Aleyrodidae	*Dialeurodes citri* (male)	3.6×10^{-5} (3)	0.0207 (6)	1.74×10^{-3} (1)	—	Present study
4. Aleyrodidae	*Trialeurodes abutilonea*	5.0×10^{-5} (4)	9.6×10^{-3} (1)	5.23×10^{-3} (7)	224.2 (152)	Present study
5. Aleyrodidae	*Aleurothrixus floccosus*	6.5×10^{-5} (5)	0.194 (5)	3.36×10^{-3} (5)	165.6 (133)	Present study
6. Aleyrodidae	*Dialeurodes citri* (female)	8.0×10^{-5} (6)	0.0264 (8)	3.03×10^{-3} (4)	—	Present study
7. Aphididae	*Aphis gossypii*	1.14×10^{-4} (7)	0.0103 (2)	0.01106 (18)	123.4 (110)	Present study
8. Aphididae	*Myzus persicae*	3.34×10^{-4} (8)	0.0237 (7)	0.01412 (22)	90.9 (94)	Present study
9. Aphididae	*Aphis fabae*	4.11×10^{-4} (9)	0.0526 (10)	7.8×10^{-3} (13)	104.7 (101)	Present study
10. Aphididae	*Aphis nerii*	4.67×10^{-4} (10)	0.0663 (13)	7.5×10^{-3} (12)	118.1 (104)	Present study
11. Aphididae	*Acyrthosiphon kondoi*	7.02×10^{-4} (11)	0.1106 (14)	6.33×10^{-3} (10)	81.1 (89)	Present study
12. Trichoceridae (2)†	*Trichocera* sp.	1.2×10^{-3}	0.200	6.00×10^{-3}	74	Sotavalta, 1952
13. Culicidae (2)	*Aedes aegypti*	1.5×10^{-3}	0.037	0.039	480	Sotavalta, 1952
14. Drosophilidae	*Drosophila virilis*	2.0×10^{-3}	0.058	0.04	240	Weis-Fogh, 1972
15. Drosophilidae	*Drosophila virilis*	2.0×10^{-3}	0.058	0.034	195	Vogel, 1966
16. Culicidae	*Culicidae* sp.	5.8×10^{-3}	0.150	0.039	277	Sotavalta, 1952
17. Culicidae	*Theobaldia annulata*	9.9×10^{-3}	0.169	0.059	262	Sotavalta, 1952
18. Anthomyiidae	*Fannia scalaris*	0.010	0.196	0.051	210	Magnan, 1934
19. Muscidae	*Musca domestica*	0.012	0.200	0.060	190	Magnan, 1934
20. Syrphidae	*Platychirus peltatus*	0.0128	0.230	0.056	147	Weis-Fogh, 1973
21. Syrphidae (3)	*Sphaerophoria scripta*	0.0193	0.200	0.094	308	Weis-Fogh, 1973
22. Syrphidae	*Syrphus grossulariae*	0.0200	0.480	0.042	114	Weis-Fogh, 1973
23. Noctuidae	*Venilia macularia*	0.021	3.400	0.006	25	Magnan, 1934
24. Apidae	*Apis* sp.	0.0213	0.20	0.11	130	Ahmad, 1984
25. Syrphidae (3)	*Syrphus corollae*	0.0213	0.350	0.061	174	Weis-Fogh, 1973
26. Syrphidae	*Syrphus nitens*	0.022	0.300	0.073	172	Weis-Fogh, 1973
27. Calliphoridae	*Calliphora erythrocephala*	0.023	0.240	0.096	160	Magnan, 1934
28. Syrphidae (7)	*Syrphus balteatus*	0.0232	0.490	0.047	138	Weis-Fogh, 1973
29. Panorpidae	*Panorpa communis*	0.030	1.750	0.017	28	Magnan, 1934
30. Tipulidae (12)	*Tipula* sp.	0.030	1.110	0.027	52	Sotavalta, 1952
31. Ichneumonidae	*Ophion luteus*	0.033	1.5501	0.021	62	Sotavalta, 1952

32. Calliphoridae	*Catabomba pirastri*	0·034	0·400	0·085	190	Magnan, 1934
33. Pieridae	*Pieris napi*	0·037	8·530	0·004	6	Sotavalta, 1952
34. Syrphidae (3)	*Syrphus ribesii*	0·0371	0·450	0·082	186	Weis-Fogh, 1973
35. Syrphidae	*Syrphus vitripennis*	0·0385	0·480	0·080	196	Weis-Fogh, 1973
36. Sphecidae	*Ammophila sabulosa*	0·045	0·420	0·11	120	Magnan, 1934
37. Sarcophagidae	*Sarcophaga carnaria*	0·045	0·36	0·125	160	Magnan, 1934
38. Satyridae	*Coenonympha pamphilus*	0·046	4·80	0·010	22	Magnan, 1934
39. Calliphoridae (12)	*Calliphora erythrocephala*	0·053	0·578	0·092	162	Sotavalta, 1952
40. Libellulidae	*Perithemis tenera*	0·061	3·812	0·016	39·4	May, 1981
41. Syrphidae	*Chrysotoxum vernale*	0·064	0·600	0·107	150	Magnan, 1934
42. Tipulidae	*Tipula gigantea*	0·069	2·260	0·030	48	Magnan, 1934
43. Syrphidae	*Eristalis arbustorum*	0·0705	0·410	0·172	211	Weis-Fogh, 1973
44. Apidae	*Euglossa saphirina*	0·071	0·35	0·20	265	Casey, May & Morgan, 1985
45. Syrphidae	*Chrysotoxum arcuatum*	0·073	0·740	0·099	144	Magnan, 1934
46. Syrphidae	*Eristalis tenax*	0·073	0·740	0·099	210	Magnan, 1934
47. Syrphidae	*Volucella pellucens*	0·073	0·780	0·094	120	Magnan, 1934
48. Syrphidae	*Chrysotoxum bicinctum*	0·075	0·680	0·110	120	Magnan, 1934
49. Apidae	*Apis mellifera*	0·078	0·420	0·186	250	Magnan, 1934
50. Apidae (4)	*Apis mellifera*	0·085	0·5878	0·145	240	Sotavalta, 1952
51. Lasiocampidae	*Malacosoma americanum*	0·088	2·36	0·04	58	Casey, 1981
52. Apidae (4)	*Euglossa mandibularis*	0·090	0·44	0·20	209	Casey *et al.* 1985
53. Vespidae (2)	*Vespa vulgaris*	0·090	0·834	0·108	143	Sotavalta, 1952
54. Apidae	*Apis mellifera*	0·1008	0·5738	0·1760	197·0	Present study
55. Lymantriidae	*Lymantria dispar*	0·101	5·39	0·02	27	Casey, 1981
56. Apidae	*Euglossa dissimula*	0·104	0·45	0·23	220	Casey *et al.* 1985
57. Lepedoptera	*Rhodocera rhamni*	0·107	12·00	0·0099	21	Magnan, 1934
58. Cantharidae	*Telephorus fuscus*	0·109	1·160	0·094	72	Magnan, 1934
59. Syrphidae	*Eristalis tenax*	0·111	0·806	0·138	164	Weis-Fogh, 1973
60. Lepedoptera	*Poecilocampa populi*	0·112	3·170	0·035	55	Sotavalta, 1952
61. Vespidae	*Polistes gallicus*	0·115	0·460	0·250	220	Magnan, 1934
62. Syrphidae	*Volucella plumata*	0·124	0·920	0·135	120	Magnan, 1934
63. Pieridae	*Pieris brassicae*	0·127	18·400	0·007	12	Magnan, 1934
64. Zygaenidae	*Zygoena filipendulae*	0·127	3·000	0·042	48	Magnan, 1934
65. Syrphidae (6)	*Eristalis tenax*	0·129	0·827	0·156	181	Sotavalta, 1952

Table 1 continued

Table 1. *Continued*

Family	Species	Mass (g)	Wing area (cm²)	Wing loading (g cm⁻²)	Wingbeat frequency (Hz)	Citation
66. Noctuidae	*Agrostis exclamationis*	0·133	3·20	0·04	41	Magnan, 1934
67. Nymphalidae	*Vanessa atalanta*	0·134	10·800	0·012	10	Magnan, 1934
68. Cerambycidae	Cerambycidae sp.	0·142	1·33	0·107	80	Sotavalta, 1952
69. Pieridae	*Pieris brassicae*	0·144	17·200	0·08	10·5	Sotavalta, 1952
70. Noctuidae	*Plusia gamma*	0·144	4·400	0·033	48	Magnan, 1934
71. Apidae	*Bombus hortorum*	0·159	0·900	0·177	135	Magnan, 1934
72. Sphingidae	*Chelonia villica*	0·165	8·000	0·021	20	Magnan, 1934
73. Corduliidae	*Tetragoneuria cynosura*	0·165	7·500	0·022	27·6	May, 1981
74. Saturniidae (5)	*Hylesia* spp.	0·168	2·334	0·072	32·4	Bartholomew & Casey, 1978
75. Apidae (6)	*Euglossa imperialis*	0·169	0·79	0·21	179	Casey *et al.* 1985
76. Nymphalidae	*Vanesa cardui*	0·173	10·400	0·017	20	Magnan, 1934
77. Libellulidae	*Erythemis simplicicollis*	0·176	8·38	0·021	28	May, 1981
78. Libellulidae	*Pachydiplax longipennis*	0·178	8·476	0·021	24·3	May, 1981
79. Vespidae	*Vespa germanica*	0·187	0·980	0·191	110	Magnan, 1934
80. Sphingidae	*Macroglossa bombyliformis*	0·189	2·620	0·072	80	Magnan, 1934
81. Nymphalidae	*Vanesa io*	0·195	14·000	0·0147	18	Magnan, 1934
82. Saturniidae (2)	*Hyperchiria nausica*	0·200	3·950	0·051	21·6	Bartholomew & Casey, 1978
83. Notodontidae	*Notodonta dictaea*	0·201	5·000	0·040	22	Magnan, 1934
84. Apidae	*Bombus muscorum*	0·226	0·900	0·251	128	Magnan, 1934
85. Diptera	*Dasyramphus atra*	0·233	1·500	0·155	100	Magnan, 1934
86. Lymantriidae	*Dasichyra pudibunda*	0·237	8·000	0·030	28	Magnan, 1934
87. Vespidae	*Vespa germanica*	0·240	1·330	0·180	139	Sotavalta, 1952
88. Libellulidae	*Libellula depressa*	0·245	13·200	0·019	20	Magnan, 1934
89. Libellulidae	*Orthetrum coerulescens*	0·248	10·800	0·023	20	Magnan, 1934
90. Scutelleridae	*Chrysocoris purpureus*	0·264	1·50	0·18	100	Ahmad, 1984
91. Tabanidae	*Tabanus bovinus*	0·276	1·840	0·150	96	Magnan, 1934
92. Nymphalidae	*Argynnis pandora*	0·278	18·00	0·015	10	Magnan, 1934
93. Libellulidae	*Sympetrum meridionale*	0·281	10·000	0·028	21	Magnan, 1934
94. Sphingidae	*Macroglossa stelatorum*	0·282	3·790	0·074	73	Sotavalta, 1952
95. Melolonthidae	*Amphimallon solstitialis*	0·291	2·290	0·127	78	Sotavalta, 1952
96. Saturniidae (4)	*Automeris jacunda*	0·298	7·572	0·039	17·1	Bartholomew & Casey, 1978

97.	Papilionidae	*Papilio podalirius*	0.300	36.000	0.008	10	Magnan, 1934
98.	Libellulidae (4)	*Leptetrum quadrimaculatum*	0.307	10.600	0.029	21	Magnan, 1934
99.	Libellulidae	*Pantala flavescens*	0.308	15.400	0.020	22.9	May, 1981
100.	Gomphidae	*Ophiogomphus serpentinus*	0.312	9.400	0.033	42	Magnan, 1934
101.	Libellulidae	*Libellula luctuosa*	0.318	13.826	0.023	19	May, 1981
102.	Sphingidae	*Macroglossa stellatarum*	0.345	4.000	0.086	85	Magnan, 1934
103.	Corduliidae	*Somatochlora tenebrosa*	0.352	12.138	0.029	25.8	May, 1981
104.	Libellulidae	*Tranea carolina*	0.358	17.900	0.020	23.6	May, 1981
105.	Libellulidae	*Plathemis lydia*	0.365	10.735	0.034	31.4	May, 1981
106.	Libellulidae	*Tramea lacerata*	0.382	18.190	0.021	26.8	May, 1981
107.	Apidae	*Bombus terrestris*	0.388	1.420	0.273	130	Magnan, 1934
108.	Sphingidae	*Enyo ocypete*	0.388	2.950	0.132	56.1	Bartholomew & Casey, 1978
109.	Saturniidae	*Automeris fieldi*	0.394	8.680	0.045	17.4	Bartholomew & Casey, 1978
110.	Apidae (2)	*Eulaema nigrita*	0.399	1.67	0.24	149	Casey et al. 1985
111.	Apidae (4)	*Eufriesia pulchra*	0.425	1.27	0.33	170	Casey et al. 1985
112.	Saturniidae (3)	*Automeris zugana*	0.428	8.297	0.052	19.0	Bartholomew & Casey, 1978
113.	Aeschnidae	*Nasiaeschna pentacantha*	0.430	16.538	0.026	21.1	May, 1981
114.	Noctuidae	*Triphoena pronuba*	0.485	7.800	0.062	24	Magnan, 1934
115.	Saturniidae	*Adelonervaia subungulata*	0.487	2.900	0.168	41.0	Bartholomew & Casey, 1978
116.	Apidae	*Bombus lapidarius*	0.495	1.650	0.300	90	Magnan, 1934
117.	Libellulidae	*Libellula pulchella*	0.508	16.387	0.031	26.2	May, 1981
118.	Aeshnidae	*Aeschna mixta*	0.530	13.80	0.04	38	Magnan, 1934
119.	Cetoniidae	*Cetonia aurata*	0.537	1.300	0.413	86	Magnan, 1934
120.	Macromiidae	*Macromia georgina*	0.545	13.974	0.039	30.0	May, 1981
121.	Apidae (6)	*Eulaema cingulata*	0.547	2.03	0.27	128	Casey et al. 1985
122.	Aeschnidae	*Brachytron pratense*	0.557	12.000	0.046	33	Magnan, 1934
123.	Sphingidae	*Xylophanes libya*	0.559	3.560	0.157	48.5	Bartholomew & Casey, 1978
124.	Saturniidae	*Automeris hamata*	0.564	5.450	0.103	23.5	Bartholomew & Casey, 1978
125.	Vespidae	*Vespa crabro*	0.567	2.600	0.218	100	Magnan, 1934
126.	Apidae (2)	*Bombus lapidarus*	0.568	1.805	0.315	152	Sotavalta, 1952
127.	Sphingidae	*Manduca lefeburei*	0.571	4.920	0.116	33.1	Bartholomew & Casey, 1978
128.	Bombycidae	*Bombyx rubi*	0.595	13.000	0.046	18	Magnan, 1934
129.	Melolonthidae	*Melolontha vulgaris*	0.597	4.450	0.134	62	Sotavalta, 1952
130.	Vespidae	*Vespa crabro*	0.597	3.040	0.196	104	Sotavalta, 1952
131.	Saturniidae	*Philosamia cynthia*	0.605	50.000	0.012	8	Magnan, 1934

Table 1 continued

Table 1. *Continued*

Family	Species	Mass (g)	Wing area (cm²)	Wing loading (g cm⁻²)	Wingbeat frequency (Hz)	Citation
132. Aeschnidae	Aeschna rufescens	0·611	17·80	0·03	20	Magnan, 1934
133. Xylocopidae	Xylocopa violacea	0·614	1·720	0·357	130	Magnan, 1934
134. Sphingidae (2)	Perigonia lusca	0·638	2·470	0·258	62·9	Bartholomew & Casey, 1978
135. Apidae (4)	Exaerete frontalis	0·644	3·48	0·19	87	Casey et al. 1985
136. Saturniidae	Automeris belti	0·665	10·960	0·061	14·4	Bartholomew & Casey, 1978
137. Sphingidae	Pachygonia drucei	0·702	4·770	0·147	48·4	Bartholomew & Casey, 1978
138. Saturniidae	Automerina auletes	0·720	8·090	0·089	23·4	Bartholomew & Casey, 1978
139. Cicadidae	Cicada sp.	0·752	7·64	0·10	42	Ahmad, 1984
140. Aeshnidae	Anax junius	0·820	21·02	0·039	20·5	May, 1981
141. Sphingidae (2)	Xylophanes pluto	0·829	4·430	0·187	45·0	Bartholomew & Casey, 1978
142. Saturniidae (3)	Adeloneivaia boisduvalii	0·839	5·564	0·151	24·9	Bartholomew & Casey, 1978
143. Apidae	Bombus terrestris	0·880	1·970	0·447	156	Sotavalta, 1952
144. Hemiptera	Tesseratoma javanica	0·926	3·88	0·239	66	Ahmad, 1984
145. Macronidae	Macronia taeniolata	0·930	20·217	0·046	25·5	May, 1981
146. Apidae (7)	Eulaema meriana	0·940	3·46	0·270	98	Casey et al. 1985
147. Melolonthidae	Melolontha vulgaris	0·961	4·020	0·239	46	Magnan, 1934
148. Saturniidae (3)	Eacles imperialis	1·105	12·600	0·088	17·9	Bartholomew & Casey, 1978
149. Aeschnidae	Anax formosus	1·200	22·80	0·053	22	Magnan, 1934
150. Sphingidae	Erinnyis ello	1·210	5·480	0·221	23·7	Bartholomew & Casey, 1978
151. Blattidae	Periplaneta americana	1·555	10·44	0·148	26	Ahmad, 1984
152. Sphingidae	Acherontia atropos	1·600	20·500	0·078	22	Magnan, 1934
153. Apidae	Bombus sp.	1·600	3·50	0·46	125	Ahmad, 1984
154. Sphingidae (4)	Manduca corallina	1·618	10·270	0·158	28·0	Bartholomew & Casey, 1978
155. Saturniidae	Syssphinx molina	1·630	9·700	0·168	22·9	Bartholomew & Casey, 1978
156. Sphingidae (2)	Madoryx oeclus	1·699	4·715	0·360	41·8	Bartholomew & Casey, 1978
157. Saturniidae	Saturnia pyri	1·890	120·000	0·016	8	Magnan, 1934
158. Lucanidae	Lucanus cervus	2·600	8·000	0·325	33	Magnan, 1934
159. Sphingidae	Manduca rustica	2·704	10·720	0·252	29·5	Bartholomew & Casey, 1978
160. Sphingidae (2)	Oryba achemenides	2·809	10·200	0·275	39·9	Bartholomew & Casey, 1978

* Numbers presented parenthetically in columns 3–6 indicate the levels of ranking, within the 160 insects tabulated, of the Homoptera studied here.

† Where a number is presented parenthetically in column 1, the values tabulated are means from several individuals in the literature. The number in parentheses indicates from how many individuals the data are derived.

Table 2. *Wing length (in mm) of measured homopterous insects*

Species		$\bar{X}$	N	Coefficient of variation (%)
Acyrthosiphon kondoi	forewing	3·39	20	3·5
	hindwing	1·93	20	5·8
Aleurothrixus floccosus	forewing	1·52	20	4·3
	hindwing	0·94	20	8·3
Aphis fabae	forewing	2·66	20	6·1
	hindwing	1·62	20	8·1
Aphis gossypii	forewing	2·18	20	7·9
	hindwing	1·37	20	9·5
Aphis nerii	forewing	2·94	20	6·6
	hindwing	1·75	20	7·0
Bemisia tabaci	forewing	0·84	20	5·6
	hindwing	0·69	20	7·2
Dialeurodes citri	forewing	1·37	20	3·6
(female)	hindwing	1·16	20	4·3
Dialeurodes citri	forewing	1·16	20	8·9
(male)	hindwing	0·93	20	4·0
Myzus persicae	forewing	3·08	20	5·2
	hindwing	1·89	20	8·5
Trialeurodes abutilonea	forewing	0·98	20	11·3
	hindwing	0·78	20	13·1
Trialeurodes vaporariorum	forewing	0·99	20	5·4
	hindwing	0·84	20	10·1

Wingbeat frequency

The two families could also be separated by wingbeat frequency (Table 1). Aphids had significantly lower wingbeat frequencies than whiteflies (range 81·1–123·4 Hz for aphids, 165·6–224·2 Hz for whiteflies) $(P < 0·01)$. Within the groups, only two aphids, *Ap. nerii* and *Ap. gossypii*, and two whiteflies, *Al. floccosus* and *B. tabaci*, had wingbeat frequencies not significantly different from one another $(P > 0·05)$.

Wing loading

Calculated wing loadings for aphids $(6·33 \times 10^{-3}$ to $0·01412 \, \mathrm{g \, cm^{-2}})$ were all larger than those of whiteflies $(1·74–5·23 \times 10^{-3} \, \mathrm{g \, cm^{-2}}$; Table 1).

Relationships between wingbeat frequency and morphometrics

Relationships between wingbeat frequency and various body morphometrics, such as wing area and length, body mass and wing loading, were evaluated for all measured insect species (exclusive of *D. citri*) (Table 3). Coefficients of determination (r^2) revealed that wingbeat frequency was most closely linked with body mass

Table 3. *Relationships between wingbeat frequency and body morphometrics for selected members of Aleyrodidae and Aphididae*

Body characteristic	Coefficient of determination r^2	F value	Significance $P<$
Forewing area	0·6939	7·43	0·05
Hindwing area	0·5569	3·60	NS
Total area	0·6651	6·35	NS
Forewing length	0·9261	48·23	0·001
Hindwing length	0·9160	41·69	0·001
Body mass	0·8275	17·37	0·005
Wing loading	0·6680	6·45	0·05

NS, not significant.

and fore- and hindwing length: 68 % of the variation in wingbeat frequency was attributable to body mass, and >80 % to length of both the forewings and hindwings. Compared with whiteflies, aphids generally have lower wingbeat frequencies and higher wing loading.

Relationships with other insects

Our homopterans weighed less than all the insects whose flight-associated morphometrics were measured in previous studies. Masses ranged from $3 \cdot 3 \times 10^{-5}$ g (*B. tabaci*) to 2·809 g (*Oryba achemenides*) (Table 1). Using total wing surface area as a criterion for size, our homopterans are among the smallest insects for whom wing loading and wingbeat frequencies have been calculated. The range of wing surface areas was from $9 \cdot 6 \times 10^{-3}$ cm^2 (*T. abutilonea*) to 120·00 cm^2 (*Saturnia pyri*). Our largest homopteran ranked only fourteenth out of 160.

The ratio of body mass to wing surface area was also low in the 11 homopterans, with five having wing loading values lower than any in the literature. The 160 insects ranged from $1 \cdot 74 \times 10^{-3}$ g cm^{-2} for male *D. citri* to 0·460 g cm^{-2} for *Bombus* spp. None of those we measured exhibited a wing loading that ranked higher than 22nd out of 160 (Table 1). For wingbeat frequencies, our homopterans exhibited some of the highest values within the recorded range of 8–480 Hz (Table 1). Rankings for whiteflies and aphids ranged from 89th to 152nd of 158.

We were also interested in the statistical relationship between body mass, wing loading and wingbeat frequency for all insects either in the literature or measured herein. Since *D. citri* was not included (for reasons discussed previously) the statistical comparisons involve 158 species. Using wing loading as the independent variable and calculating coefficients of determination for all 158 insects, we found that wing loading accounted for only 5·5 % of the variation in wingbeat frequency ($r^2 = 0 \cdot 0550$, F value = 9·08). Similar calculations using body mass as the independent variable indicate that this parameter accounted for 14 % of the variation in wingbeat frequency ($r^2 = 0 \cdot 1378$, F value = 24·92). Considering both mass (first

entry) and wing loading (second entry) as independent variables in a stepwise regression, we found that 34% of the variation in wingbeat frequency was attributable to these two parameters ($r^2 = 0.344$, F value $= 40.58$).

Relationships between body mass, wing loading and wingbeat frequency became clearer after data had been sorted according to mass. The 158 species were divided into six groups of roughly equal size. Insects weighing more than 0.03 g had to be separated into groups because slopes for regression lines for wingbeat frequency and wing loading were significantly different ($P < 0.015$) (Table 4). The slope for animals weighing 0.030–0.104 g was 1050.0, whereas the slope for insects weighing 0.720–2.809 g was 221.8. Coefficients of determination were calculated for the species within each mass group (Table 4). Examination of the F values indicated that the linear relationship between wingbeat frequency and wing loading was highly significant for all mass groups with the exception of the lightest animals (i.e. < 0.03 g) ($P < 0.001$).

The importance of excluding the smaller insects from considerations of the relationships between wingbeat frequency and wing loading became more apparent when coefficients of determination were calculated for all insect species weighing >0.03 g (Table 5). A log transformation of the independent variable, wing loading, and a log/log transformation of both the independent variable and the dependent variable, wingbeat frequency, improved the goodness-of-fit as shown by an increase in F values from 43.96 to 135.88. Similar transformation of data for insects weighing <0.03 g did little to improve the goodness-of-fit, as F values increased from 2.87 to 3.72. Log and log/log transformation for insect species in the larger mass groups decreased F values, indicating a clearly linear relationship.

We attempted to identify the relationship between wingbeat frequency and wing loading for the various taxa shown in Table 1. Although a few cases, e.g. members of Sphingidae, showed significant correlations, the majority did not. The lack of significant correlations may have been due to small sample sizes or situations where animals were arbitrarily selected because of a taxonomic relationship from groups with different slopes.

DISCUSSION

In terms of flight-associated morphometrics, the two measured families differed from one another in all important parameters considered: body mass, wingbeat frequency and wing loading. These data support the earlier observation concerning distribution of whiteflies and aphids in air columns. Our data also demonstrate that, although closely related, these insects employ different methods of flight.

The relationship between wingbeat frequency and wing loading is of special significance. The finding that whiteflies had a higher wingbeat frequency and a lower wing loading than aphids was unexpected. Other authors have argued that insects with heavy bodies in relation to total wing surface area should beat their wings more rapidly than insects of similar mass, but with larger wing surface areas (Dorsett, 1962; Bartholomew & Heinrich, 1973). This seems to be theoretically correct as well

Table 4. *Coefficients of determination for the regression equation* $y = a+bx$ *where* y = *wingbeat frequency and* x = *wing loading for all insects*

Mass range (g)	N	Coefficient of determination r^2	F value of regression	Significance P<	Slope	t value* of slope	Significance P<
0·000033–0·030	27	0·1030	2·87	NS	938·7	3·25	0·015
0·030–0·104	27	0·7780	87·56	0·001	1050·0	2·83	0·01
0·107–0·201	27	0·8904	203·17	0·001	814·7	4·54	0·001
0·226–0·399	27	0·9034	233·78	0·001	519·9	4·02	0·001
0·425–0·702	27	0·7483	74·32	0·001	333·4	3·38	0·001
0·720–2·809	23	0·6020	31·76	0·001	221·8		0·001
All insects							
0·000033–2·809	159	0·0550	9·08	0·001	186·1		

* Calculated t value for differences between slopes.
NS, not significant.

as agreeing with other authors' (Ahmad, 1984; Greenewalt, 1962) statements about birds and bats, which apparently also employ an increased wingbeat frequency tactic.

This study of wingbeat frequency and wing loading in our measured homopterans (as well as other small insects) has helped shed some light on these relationships among insects in general, about which differing conclusions have been drawn. Certain authors have concluded that wing loading and wingbeat frequency are significantly correlated, especially if wing lengths are part of the equation (e.g. May, 1981). Others, such as Bartholomew & Casey (1978), are less certain of such a relationship and suggest that it is variable. Finally, others (Casey, May & Morgan, 1985) state no such relationship could be established for insect species they studied.

Our data demonstrate that among groups of larger insects wingbeat frequency and wing loading are significantly correlated, conforming to the hypothesis that animals with high wing loading compensate by using higher wingbeat frequencies. The differences in the steepness of the slopes of regression lines for each group indicate that smaller insects employ increased wingbeat tactic at rates exponentially higher than for larger insects.

Previous authors whose data failed to indicate a correlation between these two parameters may have considered either too few subjects or mixed insect species whose body masses were dramatically different. Casey *et al.* (1985) measured euglossine bees and showed that their wingbeat frequencies were inversely correlated with wing length and mass, but not with wing loading. We incorporated their data on bees into our larger data set, selecting groups of the same size as those used in our calculations (i.e. 26 ± 2), which included their insects. The correlation between wing loading and wingbeat frequency for the groups was highly significant for each ($P < 0.001$) (Table 6). Similar incorporations and recalculations were made using the data for members of the Sphingidae and Saturniidae generated by Bartholomew

Table 5. *Coefficient of determination for log transformations where* $y = $ *wingbeat frequency and* $x = $ *wing loading*

Mass range (g)	Coefficient of determination r^2	F value	Significance $P<$
3.3×10^{-5} to 2·809 (all insects)			
no transformation	0·0550	9·08	0·003
log transformation of x	0·0623	10·36	0·002
log/log transformation	0·3831	26·68	0·001
0·03–2·809 (without smallest insects)			
no transformation	0·2542	43·96	0·001
log transformation of x	0·3498	69·41	0·001
log/log transformation	0·6489	135·87	0·001
3.3×10^{-5} to 0·03 (smallest insects)			
no transformation	0·1030	2·87	0·1
log transformation of x	0·1227	3·49	0·073
log/log transformation	0·1294	3·72	0·065

Table 6. *Relationship between wingbeat frequency and wing loading among members of Apidae, Saturniidae and Sphingidae determined after combining referenced data*

Family	N	Mass range* (g)	Coefficient of determination r^2	F value	Significance P<
Apidae	26	0·071–0·144	0·8369	123·11	0·001
	26	0·144–0·291	0·8836	182·16	0·001
	26	0·298–0·547	0·7212	62·09	0·001
	25	0·557–0·940	0·8392	120·04	0·001
Saturniidae	28	0·168–0·318	0·8879	205·86	0·001
	27	0·345–0·595	0·7159	62·99	0·001
	27	0·597–1·631	0·7573	78·07	0·001
Sphingidae	27	0·388–0·638	0·7280	66·93	0·001
	26	0·644–2·809	0·5712	31·37	0·001

* Data from Table 4.

& Casey (1978). Results were the same, i.e. correlations between wingbeat frequency and wing loading were highly significant ($P < 0·001$) (Table 6).

For very small insects, the lack of relationship may be explained by the fact that some minute species solve the problem of staying aloft in unique ways. Some, like whiteflies (Wootton & Newman, 1979) and *Drosophila* (Weis-Fogh, 1972), employ a clap and fling mechanism to generate extra lift. This reduces the need for exceptionally high wingbeat frequencies, and agrees with the data presented here. Our data also support Pringle's (1976) correct prediction that, because they have exceptionally low wing loadings, whiteflies would not have the high wingbeat frequencies commonly associated with small insects (e.g. 480 Hz for *Aedes aegypti*; Table 1). Whitefly wingbeat frequencies are rather more correctly characterized as being mid-range (here 165·6–224·2 Hz; Table 1). The same strategy may be employed by other insects weighing <0·03 g. A third possibility is that many small insects accomplish flight in a manner similar to that reported for aphids (Haine, 1955), i.e. by relying to a large extent on an ability to use wind currents passively. Being small, they have low settling velocities because of high drag coefficients. Any of these strategies would help explain why small insects may not conform to the generalization that animals with high wing loading have a high wingbeat frequency (e.g. members of Hymenoptera) and that insects with low wing loading have a low wingbeat frequency (e.g. members of Lepidoptera). Any group of small insects may contain several statistical 'outliers', resulting in a lack of relationship between wingbeat frequency and wing loading.

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