J. Indian Inst. Sci., July–Aug 1991, 71, 365–372.

Morphometrics and wing-stroke frequency of bumblebees

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Received on October 31, 1989; Revised on December 10, 1990, and May 6, 1991.

Abstract

A study of wing-beat frequency of *Bombus asiaticus* Morawitz and *B. albopleuralis* Friese shows that while the frequency varies between individuals and species, and is a function of body parameters, in general, the former has higher wing-beat frequency compared to the latter. *B. asiaticus* has greater weight and size than *B. albopleuralis*. Experimental results agree with theoretically computed values obtained from mass-flow theory.

Key words: Morphometrics, *Bombus asiaticus, B. albopleuralis,* wing-beat frequency, pollination efficiency.

1. Introduction

Bumblebees, *Bombus asiaticus* and *B. albopleuralis* are acknowledged pollinators of several crops[1]. Apart from various other factors such as abundance of pollinating insects, rate of flower visitation and pollen-carrying capacity, the pollinating efficiency of a bee depends upon its speed of flight and the rate at which it flies from one flower to another. Since wing-beat frequencies express the flight intensity of fliers, its evaluation may help in assessing their pollinating efficiency[2]. This paper reports on the wing-beat frequency of *B. asiaticus* and *B. albopleuralis* and compares the experimentally determined frequency with the theoretically computed values using mass-flow theory.

2. Materials and methods

Bumble bees were collected during July-August, 1986, while visiting red clovers at Harwan, Srinagar, India. The wing-beat frequencies were determined by an acoustic technique[3] with some modifications. They were recorded with a dynamic microphone (Model, Piezo Dynamic) and a tape recorder (Model, AM 124 Philips), kept outside the bioclimatic chamber and operated remotely using a pickup microphone (Fig. 1).

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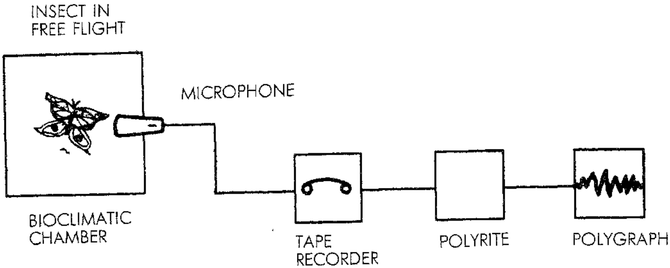

FIG. 1. Schematic set-up for recording and analysis of insect flight sounds.

The flight sounds were played into a polygraph-oscillating pen recorder (Model 8, Recorders and Medicare Systems, Chandigarh, India) that displayed the frequencies on the paper as sine waves with each unit representing the wing-beat frequencies per second. Five measurements of wing-beat frequencies were made per individual for each test situation. The mean and standard error was calculated for each bee based on the five wing-beat frequency measurements. The weight of each test bee was determined to the nearest 0·1 mg by a single pan analytical balance. Wing length and wing span were measured to the nearest 0·01 cm. The wing area was measured by clipping the wings and arranging them on a square centimetre graph and counting the squares enclosed. These body parameters were then used to compute the expected wing-beat frequency following Puranik *et al*[4] as follows:

$$V_h = \frac{K \times M_f}{L^2 \times B_{eff}}$$

where,

V_h = wing-beat frequency in hovering state,

M_f = mass of the flier,

B_{eff} = the effective wing breadth $= \dfrac{\text{wing area } (a)}{\text{wing length } (l)}$,

l (wing length) = the length from the joint to tip of the wing,

L (wing span) = the length from the tip of one wing to the tip of the other,

K = proportionality constant $= \dfrac{8g}{\rho K} = 2086$,

g = acceleration due to gravity, and

ρ = the density of the medium in which the flier is hovering (0·0011 g/cc).

The value of K is obtained by drawing a curve between mass of the flier and $V_o \times L^2 \times B_{eff}$. If this curve is found to be linear and passes through the origin then the theory is valid. The value of K is obtained from the slope and used for further computing the wing-beat frequency of the fliers.

Wing loading is calculated using the formula:

$$= \frac{\text{Body mass } (g)}{\text{Total wing area } (\text{cm}^2)},$$

and the surface area of the wings or aspect ratio is calculated using the formula:

$$\frac{(\text{Wing length})^2(\text{cm}^2)}{\text{Total wing area } (\text{cm}^2)}.$$

The relationship between the mass of the fliers and other body parameters is calculated by a simple regression analysis, and the differences between body parameters and wing-beat frequencies of the two species are compared by students' t-distribution. The experimental and theoretically calculated values of wing-beat frequencies are compared using χ^2 test following Snedecor and Cochran[5].

3. Results and discussion

3.1. *Comparison between experimental and theoretical wing-beat frequency*

Experimentally determined wing-beat frequencies (V_o) of *B. asiaticus* and *B. albopleuralis* along with body parameters (Table I) show that wing-beat frequencies vary from a minimum of 149·55 cps (*B. albopleuralis*) to a maximum of 218·75 cps (*B. asiaticus*) between individuals and species.

The results differ from the studies made by Puranik *et al*[4] and Kammer and Heinrich[6] who reported considerably lower values. The large differences between their values and the present investigation may be due to differences in bee species, physiological state of the insects and recording methods. The data in Tables I and II further reveal that experimental values of wing-beat frequencies agree with theoretically claculated values thus further confirming the results (χ^2, $P \leqslant 0{\cdot}05$). The data further show that the ratio of experimental values to theoretical values approximated unity. This result corroborates the findings of earlier investigators[2-4].

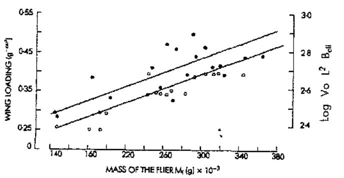

FIG. 2. Relationship in *Bombus asiaticus* between mass of the flier and i) wing loading $r = 0{\cdot}843$, $p < 0{\cdot}01$, $Y = 0{\cdot}166 + 0{\cdot}0009X$; ii) product of observed wing-beat frequency (V_0), square of the wing span (L^2) and effective wing breadth (B_{eff}) $r = 0{\cdot}780$, $P < 0{\cdot}01$, $Y = 2{\cdot}25 + 0{\cdot}0017X$. Wing loading (●), log V_0 $L.B_{eff}$(o).

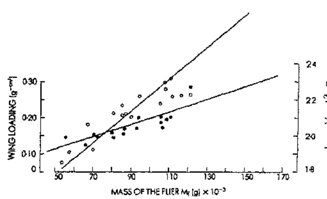

FIG. 3. Relationship in *B. albopleuralis* between mass of the flier, and i) wing loading $r = 0{\cdot}841$, $P < 0{\cdot}01$, $Y = 0{\cdot}0395 + 0{\cdot}0015\,X$; ii) product of the observed wing-beat frequency (V_0), square of the wing span (L^2) and effective wing breadth $r = 0{\cdot}961$, $P < 0{\cdot}01$, $Y = 1{\cdot}671 + 1{\cdot}0064X$. Wing loading (●) log V_0 $L.B_{eff}$ (o).

3.2. *Relationship between body parameters and the mass of the fliers*

To check the validity of mass-flow theory, the relationship between body parameters and mass of the fliers was computed by simple correlation analysis. Figures 2 and 3 show that the relationship is highly significant indicating the pronounced influence of body parameters and the mass of the fliers on the wing-beat frequency or flight efficiency of insects. Further, body parameters like the product of the square of the span, effective wing breadth and observed wing-beat frequency (V_o), when plotted against the mass of the fliers (M_f), exhibit linear relationship. This is also true in both the species when wing loading (M_f/A) is plotted against the mass of the fliers (M_f). The linear relationship obtained in both the instances reveals that the proposed theory is valid and can be used for computing theoretical wing-beat frequencies. In earlier studies also, such relationship was observed by Abrol and Kapil[2] in the case of honeybees and solitary bees and by Puranik *et al*[4] in the case of honeybees, bumblebees and solitary bees.

3.3. *Wing-beat frequency in relation to body size*

Data (Table I) show that smaller bees (per gram of body weight) have higher wing-beat frequency than the larger ones. For instance, *B. albopleuralis* (Av. 89·10 mg, n=20) exhibited 1700 cps per gram of body weight, whereas in the case of *B. asiaticus* (Av. 265·00 mg, n=20) it was 800 cps, a difference of more than two fold (calculated values). This may be due to smaller surface area of wings (9·53, n=20) in the case of the former than the latter (14.81, n = 20) (Table II). This shows that because of the smaller surface area of the wings, the bees must beat rapidly to be in flight. Evidently, large-bodied insects are generally slow fliers than the smaller ones. Similar results were obtained by Abrol and Kapil[2], and Kammer and Heinrich[6] who found that smaller insects per gram of body weight had higher wing-beat frequency than the larger ones. The data presented in Tables I and II further show that wing-beat frequencies varied inter- and intra-specifically. For instance, wing-beat frequencies of some individuals of *B. asiaticus* are even equal to *B. albopleuralis* (Table I). This shows that wing-beat frequencies alone cannot be species specific and as such no generalization can be drawn. The data further reveal that body parameters differ significantly between the two species (t test, $P \leq 0{\cdot}01$). This is also true when the wing-beat frequencies are compared between the two species (t test, $P \leq 0{\cdot}01$). Since the body parameters are different in both the species, it can be concluded that wing-beat frequencies along with body parameters are species specific. The present investigation corroborates the earlier observations[2,4] that wing-beat frequencies, along with body parameters, are species specific. This study also supports the contention of Reed *et al*[7] that wing-beat frequencies of insects can be used to characterize ecotypes or identification of the species.

3.4. *Wing loading and aspect ratio in relation to flight efficiency of bees*

The data in Table II show that the range of wing-loading values is 0·1288 – 0·2727 g cm^{-2} for *B. albopleuralis* and 0·2900 – 0·5178 g cm^{-2} for *B. asiaticus*. The range obtained for aspect-ratio or flight surfaces is 4·09 – 12·25 for the former and 9·80 – 22·26 for the latter. Similar values are reported in literature for honeybees,

Table I

Comparison of experimental and theoretically computed wing-beat frequency of females of *B. asiaticus* and *B. albopleuralis*

No. of observations	Mass of the flier $M_f(g) \times 10^3$	Observed wing-beat frequency (V_o) Mean	Observed wing-beat frequency (V_o) SE	Wing span L(cm)	B_{eff} (cm)	$L^2 \times B_{eff}$ (cm)	$V_o L^2 \times B_{eff}$ (cm)	Frequency $V_h = K \times M_f / L^2 \times B_{eff}$	V_h/V_o
B. asiaticus									
1	145·00	180·00	4·19	3·00	0·1912	1·730	311·40	174·83	0·97
2	320·00	240·00	1·64	2·80	0·3330	2·610	626·40	255·75	1·06
3	290·00	344·00	3·62	2·80	0·2150	1·685	579·64	359·01	1·04
4	265·00	232·00	4·20	3·20	0·2330	2·385	553·32	231·77	0·99
5	180·00	150·00	1·82	3·20	0·1916	1·961	194·15	191·47	1·27
6	290·00	262·00	2·83	2·90	0·2660	2·237	586·09	270·42	1·03
7	265·00	210·00	3·10	3·10	0·3070	2·950	619·50	187·38	0·89
8	340·00	212·00	4·12	3·60	0·2370	3·071	651·05	230·94	1·08
9	260·00	220·00	3·10	2·90	0·2700	2·270	499·40	238·92	1·08
10	200·00	180·00	2·83	2·90	0·2500	2·102	378·36	198·47	1·10
11	245·00	200·00	1·94	3·40	0·2230	2·577	515·40	198·31	0·99
12	315·00	260·00	4·24	2·90	0·3070	2·581	671·06	254·48	0·97
13	300·00	220·00	2·17	3·20	0·2660	2·723	599·06	229·82	1·04
14	360·00	245·00	3·48	3·30	0·3070	3·343	819·03	224·63	0·91
15	250·00	210·00	3·27	3·00	0·2462	2·214	464·94	235·54	1·12
16	280·00	220·00	2·27	2·90	0·2916	2·454	539·44	238·20	1·08
17	190·00	150·00	1·47	3·10	0·2461	2·365	354·75	167·58	1·11
18	240·00	195·00	2·46	3·20	0·2833	2·900	565·50	172·63	0·88
19	310·00	240·00	2·94	2·90	0·3083	2·592	622·08	249·48	1·03
20	255·00	205·00	3·17	3·10	0·2916	2·802	574·41	189·83	0·92
Mean	265·00	218·75		3·07	0·2632	2·477	541·24	224·97	1·02
SE	12·33	9·57		0·047	0·004	0·421	28·95	9·85	0·005
$\chi^2 \leqslant 0{\cdot}005$									
B. albopleuralis									
1	80·00	120·00	1·17	2·20	0·2777	1·344	161·28	124·16	1·03
2	92·00	142·50	2·01	2·30	0·2000	1·058	150·76	181·39	1·27
3	86·00	150·00	1·87	2·20	0·2250	1·089	163·35	164·73	1·09
4	70·00	135·00	1·17	2·00	0·2300	0·920	124·20	158·71	1·17
5	56·00	130·00	2·31	2·10	0·1500	0·661	85·99	176·59	1·35
6	80·00	140·00	1·87	2·30	0·2250	1·190	166·60	140·23	1·00
7	120·00	220·00	2·10	2·30	0·1833	0·969	213·31	258·16	1·17
8	72·00	150·00	1·87	2·10	0·2285	0·914	137·13	164·28	1·09
9	92·00	170·00	1·47	2·20	0·2454	1·187	201·77	161·67	0·95
10	108·00	185·00	1·84	2·30	0·2500	1·322	244·57	170·41	0·92
11	110·00	170·00	2·13	2·30	0·2240	1·184	201·28	193·00	1·14
12	105·00	154·00	1·81	2·20	0·2416	1·169	180·02	187·00	1·21
13	86·00	130·00	1·94	2·10	0·2653	1·284	166·92	139·71	1·07
14	107·00	154·00	0·42	2·30	0·2800	1·482	228·81	150·71	0·97
15	150·00	140·00	1·72	2·30	0·2700	1·428	199·92	153·38	1·09
16	58·00	118·50	2·08	2·00	0·2315	0·926	109·92	130·61	1·10
17	67·00	135·20	1·16	2·05	0·2653	1·114	150·61	125·45	0·92
18	84·00	140·00	1·43	2·20	0·2550	1·234	172·76	141·09	1·01
19	98·00	150·00	2·43	2·25	0·2476	1·253	18·95	163·15	1·08
20	106·00	156·40	1·87	2·30	0·2800	1·481	231·62	149·30	0·95
Mean	89·10	149·55		2·20	0·2387	1·158	173·93	161·70	1·08
SE	4·09	5·26		0·007	0·008	0·050	9·25	6·68	0·05
$\chi^2 \leqslant 0{\cdot}005$									

Table II
Aerodynamic parameters of *B. asiaticus* and *B. albopleuralis*

No. of observations	Mass of the flier $M_f(g) \times 10^{-3}$	Wing span, L (cm)	Total wing area, L (cm^2)	Aspect ratio L^2/a	Wing loading M_f/a ($g.cm^{-2}$)	Mass $\overline{(\text{Wing span})^2 M_f/l}$
B asiaticus						
1	145·00	3·00	0·50	18·00	0·2900	0·0161
2	320·00	2·80	0·80	9·80	0·4000	0·0408
3	290·00	2·80	0·56	14·00	0·5178	0·0369
4	265·00	3·20	0·56	18·28	0·4732	0·0258
5	180·00	3·20	0·45	22·26	0·3913	0·0175
6	290·00	2·90	0·64	13·14	0·4531	0·0344
7	356·00	3·10	0·80	12·01	0·3312	0·0275
8	340·00	3·60	0·75	17·05	0·4473	0·0262
9	260·00	2·90	0·54	15·57	0·4814	0·0309
10	200·00	2·90	0·60	14·01	0·3333	0·0237
11	245·00	3·40	0·58	19·93	0·4224	0·0211
12	315·00	2·90	0·74	11·36	0·4256	0·0375
13	300·00	3·20	0·64	16·00	0·4687	0·0292
14	360·00	3·30	0·80	13·61	0·4500	0·0330
15	250·00	3·00	0·64	14·06	0·3906	0·0277
16	280·00	2·90	0·70	12·01	0·4000	0·0332
17	190·00	3·10	0·64	15·01	0·2968	0·0197
18	240·00	3·20	0·68	15·05	0·3529	0·0234
19	310·00	2·90	0·74	11·36	0·4189	0·0368
20	255·00	3·10	0·70	13·72	0·3642	0·0263
Mean	265·00	3·07	0·65	14·81	0·405	0·0284
SE	12·33	0·047	0·028	0·695	0·014	0·0015
B. albopleuralis						
1	80·00	2·20	0·50	9·60	0·1600	0·01652
2	92·00	2·30	0·48	11·02	0·1916	0·01739
3	86·00	2·30	0·54	8·96	0·1592	0·01776
4	70·00	2·00	0·46	6·69	0·1521	0·01750
5	56·00	2·10	0·36	12·25	0·1555	0·01269
6	80·00	2·20	0·54	9·79	0·1481	0·01512
7	120·00	2·30	0·44	12·02	0·2727	0·02260
8	72·00	2·10	0·48	9·18	0·1500	0·01632
9	92·00	2·20	0·54	8·96	0·1703	0·01900
10	108·00	2·30	0·60	8·81	0·1800	0·02041
11	110·00	2·30	0·56	9·44	0·1964	0·02079
12	105·00	2·30	0·58	8·34	0·1810	0·02169
13	86·00	2·10	0·52	8·44	0·1653	0·01950
14	107·00	2·30	0·56	9·44	0·1910	0·02022
15	105·00	2·30	0·54	9·79	0·1944	0·19444
16	58·00	2·00	0·44	9·09	0·1318	0·01450
17	67·00	2·05	0·52	8·08	0·1288	0·01594
18	84·00	2·20	0·50	9·68	0·1680	0·01735
19	98·00	2·25	0·52	9·73	0·1884	0·01935
20	106·00	2·30	0·52	9·44	0·1892	0·02003
Mean	89·10	2·20	0·51	9·53	0·1737	0·01823
SE	4·09	0·007	0·043	0·843	0·015	0·0018

bumblebees and solitary bees[2,4]. Critical examination of the data further revealed that wing loading is comparatively higher in *B. asiaticus* than *B. albopleuralis* thereby reflecting that the former species is relatively fast flier than the latter. Similar results were obtained by Ahmed[8] who found that megachiropteran bats having higher wing loading than microchiropteran bats are relatively fast fliers. Like wing loading, aspect ratio or flight surface area is higher in *B. asiaticus* than *B. albopleuralis*. This shows that former species exhibits superior manoeuvering capabilities than the latter. The results agree with those of Ahmed[8] who found that smaller birds, bats and insects such as *Bombus* sp. and *Apis* sp. having higher aspect ratio than larger birds and other insects are efficient in manoeuvering. The data presented in Table I further reveal that bumblebees are equipped with a flight apparatus which has either low wing loading coupled with low aspect ratio (*B. albopleuralis*) or higher wing loading with higher aspect ratio (*B. asiaticus*). The data (Table II) also show that wing loading per unit aspect ratio remains constant irrespective of the wing loading and aspect ratio values.

This study shows that aerodynamic parameters such as wing loading, aspect ratio and wing-beat frequencies influence the behaviour and flight efficiency of insects. The wing-beat frequencies, along with body parameters which are species specific, may help in characterization of ecotypes or isolation of species. This investigation suggests that *B. asiaticus* is a faster flier than *B. albopleuralis* and may be efficient pollinator as reported in earlier studies[1,9].

Acknowledgement

The author wishes to thank the Head, Division of Entomology, Sher-e-Kashmir University of Agricultural Sciences and Technology, Srinagar, for necessary facilities, Dr P.K. Dwarakanath, Professor and Head, Department of Veterinary Physiology, Haryana Agricultural University, Hisar, for polyrite facilities. Thanks are also due to the Editor and anonymous reviewers for their constructive criticism and many helpful suggestions on an earlier draft of this paper.

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