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THE WINGS OF INSECTS AND BIRDS AS MECHANICAL OSCILLATORS

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IN the course of a study of the flight of hummingbirds, I have taken several hundred high-speed moving picture sequences of the female ruby throat (*Archilochus colubris*) under a great variety of flight conditions. The sequences include hovering flight, flight at linear velocities up to thirty miles per hour—the top speed of which these birds are capable—take-offs from a perch, and escape routines when the birds became frightened. For all of these conditions the wing beat frequency remained constant at 53 ± 3 wing beats per second.

The constancy of wing beat rate pointed strongly to the possibility that these frequencies for hummingbird wings, and perhaps for insects and birds generally, could be explained as characteristic frequencies of driven damped oscillators.

The motion of such oscillators, assumed to be harmonic, is described by the following differential equation ($\dot{\varphi} = d\varphi/dt$, etc.).

$$I\ddot{\varphi} + B\dot{\varphi} + fr = F_0 r \cos \omega t, \quad (1)$$

where

- I is the moment of inertia of the oscillator,
- B the damping parameter, which accounts for the external and internal damping resistance assumed to be proportional to the angular velocity of the oscillator,
- f the harmonic restoring force,
- F_0 the amplitude of the driving force,
- r the effective radius of attack of f and F_0 ,
- ω the frequency of the driving force ($\omega = 2\pi\nu$, where ν is the number of oscillations per unit time),
- φ the angular displacement, and
- t time.

In applying this model to birds or insects, I is to be identified with the sum of the external and internal moments of inertia. The external moment of inertia is that of the wing I_w , the

internal, I_{int} , that of the muscle and whatever portion of bone, tissue, and external skeleton oscillates with it. B is the damping parameter due to internal "friction" and to external air resistance. $F_0 r$ is the amplitude of the moment exerted by the muscular driving force derived from muscle chemistry.

The restoring moment fr must be related to the elastic properties of muscle tissue. Let us assume that the muscle elasticity can be described by the force-extension relation of elastic polymers such as rubber, in the Gaussian-network approximation.

$$f = G_0 A_0 (\beta - \beta^{-2}), \quad (2)$$

where G_0 is the elastic modulus of the muscle, A_0 the cross section of the unstrained muscle, and β the extension ratio b/b_0 , where b and b_0 are the length of the strained and unstrained muscle relative to the equilibrium position $\varphi = 0$, respectively.² For small extension ratios, the expression $(\beta - \beta^{-2})$ reduces to $\sim 3\Delta b/b_0$, so that with $G = 3G_0$,

$$f = GA_0 \frac{\Delta b}{b_0}. \quad (2a)$$

We assume further that A_0 is proportional to b_0^2 , and Δb to $r\varphi$. Then,

$$f = Kb_0 r \varphi, \quad (3)$$

where K is a proportionality constant.

The characteristic frequency of the system described by eq. (1), when free and undamped, i.e., when $B = 0$ and $F_0 = 0$, is given by eq. (4).

$$\omega_0^2 = \frac{Kb_0 r^2}{I}. \quad (4)$$

The work, W , done by the driving force F_0

² Recently, Machin and Pringle (1959) reported experimental force-extension curves of insect muscles which in fact can be interpreted over their entire range in terms of the theory of rubber elasticity for non-Gaussian networks, applicable for strains up to the maximum extension of a molecular network. For moderate strains, eq. (2) follows directly from this theory.

¹ I must express my deep appreciation to Dr. Werner Brandt who undertook cheerfully the difficult and I fear unrewarding task of instructing me in the mathematics of oscillator theory, and who made many other helpful contributions in the preparation of this paper.

against the damping resistance, is

$$W = \int B \dot{\varphi} d\varphi = \Phi_0^2 B \omega^2 \frac{t}{2} \quad (5)$$

where t is long compared to the time for a single wing beat. Φ_0 is given by eq. (6)

$$\Phi_0 = \frac{F_0 r}{[I^2(\omega_0^2 - \omega^2)^2 + B^2 \omega^2]^{1/2}} \quad (6)$$

Combining eqs. (5) and (6)

$$W = \frac{F_0^2 r^2 B \omega^2 t}{2[I^2(\omega_0^2 - \omega^2)^2 + B^2 \omega^2]} \quad (7)$$

The mechanical work is thus dependent only on amplitude and frequency of the wing beat, and on the damping parameter B corresponding to a given flight regime. However, the muscular driving force F_0 will be at a minimum when $\omega = \omega_0$. Since provision of the force F_0 is certainly associated with energy expenditure in the muscle, it follows that muscular energy will be at a minimum when the muscular driving force is in resonance with the characteristic frequency of the undamped system. Because of eq. (4), the wing beat rates of insects and birds should be essentially independent of both external and internal loading.

As direct evidence that wing beat frequencies are indeed unaffected by the external load, we

cite (1) the results with the female ruby throat described in the opening paragraph, (2) experiments with insects flying in air at various sub-atmospheric pressures which show little or no change in wing frequency as the air pressure (external wing loading) is reduced.³

We take these observations to confirm that in general, for maximum economy in energy expended, the wings of flying insects and birds beat at the characteristic frequency of the undamped system, regardless of loading.

Sotavalta (1952 and 1954) gives a mass of valuable data which permit a conclusive test of the validity of eq. (4) for the unarticulated wings of insects. For a large number of insect species he clipped progressively larger pieces from the wings of a given insect and measured both wing frequency and moment of inertia of the residual wing segment. He carried the mutilation process to the point that wing segments at the end of a series of experiments were vestigial.

³ Sotavalta (1952) finds an increase in wing frequency with decreasing air pressure for some insects; for others there is no effect. Where the effect exists it is small, never more than a 15 per cent increase in wing frequency for a decrease in air pressure from 1 to 0.1 atmosphere. This behavior also is in accord with oscillator theory, if we assume W and Φ constant and $F \leq F_0$. From eqs. (5) and (7) we derive the expression

$$\frac{1}{c(c-1)} \leq \frac{I^2 \omega_0^2}{B_0^2},$$

where $c \equiv \omega^2/\omega_0^2$ and the subscript zero refers to the resonance condition. One infers from this equation that the larger the value of the right-hand term the more closely the insect or bird is bound to its resonance frequency. Now if $I \sim l^5$ and $B \sim l^4$, the larger $\omega_0 l = 2\pi\nu_0 l$ the smaller the permissible departure from resonance without exceeding F_0 . The following table is based on Sotavalta's data.

Insect	$\nu_0 l$	Effect of reducing atmospheric pressure
<i>Apis mellifica</i>	2,390	None
<i>Bombus terrestris</i>	2,700	None
<i>Vespa vulgaris</i>	1,830	None
<i>Vespa germanica</i>	1,250	None
<i>Calliphora erythrocephala</i>	1,760	None
<i>Eristalis tenax</i>	2,460	None
<i>Aedes aegypti</i>	1,260	Positive but very small
<i>Ophion</i> sp.	930	Positive
<i>Trichocera</i> sp.	480	Positive
<i>Tipula</i> sp.	850	Positive
<i>Pieris brassicae</i>	360	Positive
<i>Nemeritis canescens</i>	590	Positive
<i>Drosophila</i> sp.	370	Positive

For all insects showing a positive correlation between air pressure and wing frequency, $\nu_0 l$ is substantially smaller than the value for those showing no effect.

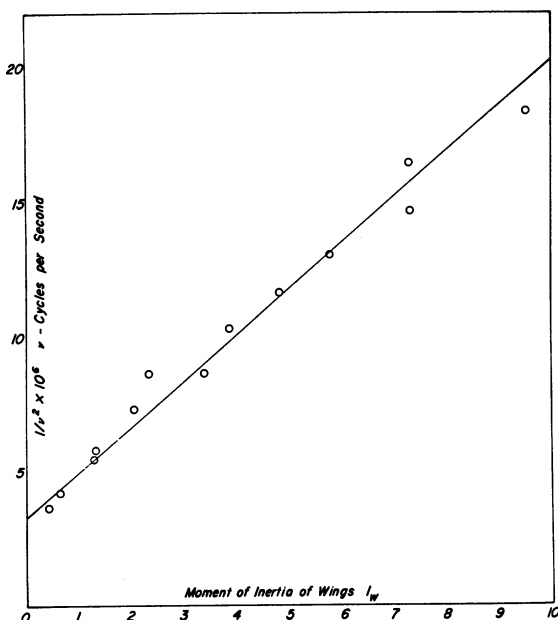


FIG. 1. Data from Sotavalta (1952) for two specimens of *Apis mellifica*.

We write eq. (4) as follows.

$$I_w + I_{int} = K'b_0r^2\nu^{-2}, \quad (8)$$

where $K' = K/4\pi^2$. For any given insect, I_{int} and $K'b_0r^2$ are constants. Hence, if one plots I_w as a function of ν^{-2} , a straight line should result, with an intercept at $I_w = 0$ corresponding to the characteristic frequency of the muscle system alone, with the slope $K'b_0r^2$. I_{int} can be extracted from the values of intercept and slope. A typical plot is shown in figure 1, based on Sotavalta's data for *Apis mellifica*. The results of this interpretation for all insects studied by Sotavalta (1952 and 1954) are given in table 1.

Roeder (1951) has classified insects as "synchronous" or "asynchronous," depending on the coincidence, or lack of it, between muscular spike potentials and wing beats. For such insects as *Periplaneta* and *Agrotis* he observes one spike potential per wing beat. For *Vespa* and *Calliphora*, on the other hand, each muscular spike potential is associated with from 5 to 20 wing beats. His data also appeared to show that for synchronous insects amputation of the wings had little effect on wing beat rate. Sotavalta (1954) performed systematic wing mutilations on a group of "synchronous" insects. He was kind enough to send me his original data, which

TABLE 1

Insect	ν (sec ⁻¹)	I_w	I_{int}	$K'b_0r^2$ (10 ⁻² erg)	M_i (mg)	M_w (mg)
		(mg mm ²)				
Asynchronous insects—Sotavalta (1952)						
<i>Apis mellifica</i>	240	8.40	2.0	6.0	97	0.425
<i>Theobaldia annulata</i>	262	0.63	0.11	0.5	9.9	0.065
<i>Bombus lapidarius</i>	143	131	18.1	29.6	477	2.465
<i>Bombus terrestris</i>	156	158	19.8	40.3	880	2.860
<i>Melolontha vulgaris</i>	62	1,180	34	42.1	597	8.955
<i>Eristalis tenax</i>	175	15.9	3.0	5.65	50	0.655
<i>Eristalis tenax</i>	185	31.0	6.2	11.7	206	0.985
<i>Calliphora erythrocephala</i>	180	1.39	0.46	0.57	15	0.170
<i>Calliphora erythrocephala</i>	154	12.6	2.8	3.5	62	0.638
<i>Calliphora erythrocephala</i>	156	17.8	4.3	5.36	100	1.015
<i>Tipula</i> sp.	63	29.0	6.4	1.35	21	0.460
<i>Tipula</i> sp.	42	100	7.0	1.89	35	0.865
<i>Tipula</i> sp.	63	44.1	7.7	2.14	30	0.655
<i>Tipula</i> sp.	49	86.2	7.7	2.14	34	0.890
<i>Tipula</i> sp.	49	55.7	6.4	1.35	21	0.720
<i>Tipula</i> sp.	63	13.9	2.8	0.64	20	0.465
<i>Tipula</i> sp.	49	132	11.5	4.28	75	1.385
<i>Tipula</i> sp.	48	71.4	7.3	1.83	23	0.930
<i>Tipula</i> sp.	48	74.6	7.0	1.89	22	0.875
<i>Tipula</i> sp.	48	51.5	6.4	1.35	22	0.785
<i>Vespa germanica</i>	139	69.6	12.0	15.0	240	1.390
<i>Vespa vulgaris</i>	143	26.0	5.2	5.34	81	0.665
<i>Trichocera</i> sp.	67	0.674	0.082	0.033	1.57	0.050
<i>Ophion luteus</i>	62	32.2	4.8	1.32	33	0.675
<i>Cerambycidae</i> sp.	80	68.8	9.1	5.1	142	1.845
<i>Pieris brassicae</i>	10.5	4,230	2,010	7.30	144	17.975
Synchronous insects—Sotavalta (1954)						
<i>Agrotis ypsilon</i>	51	498	234	16.7	169	6.27
<i>Amphitrota clandestina</i>	45	541	508	20.3	150	6.29
<i>Amphitrota clandestina</i>	48	701	582	29.1	—	7.83
<i>Sideridis unipuncta</i>	41	548	109	11.5	—	6.88
<i>Sideridis unipuncta</i>	46	233	292	10.8	111	3.03
<i>Amathes bicolorago</i>	53	111	123	6.17	82	2.30
<i>Sympetrum danae</i>	41	640	603	21.0	90	4.4
<i>Poecilocampa populi</i>	55	265	252	14.8	112	5.23

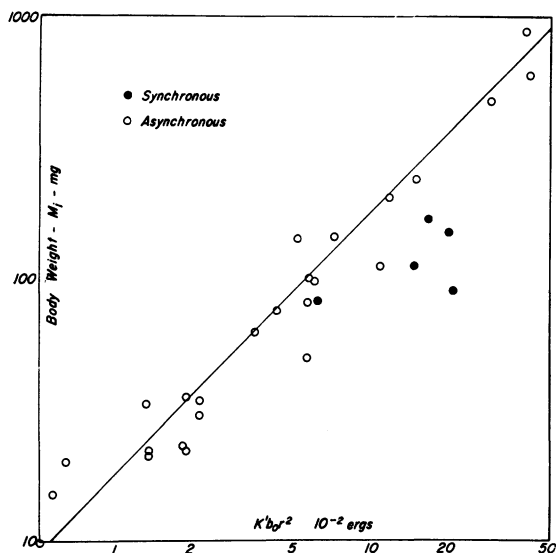


FIG. 2. Muscular restoring force and body weight. Data from table 1. The point for *Trichocera* sp. is not plotted. It is anomalous, perhaps because of the uncertainty, for so tiny an insect, in the measurement of weights of body and wings.

I have treated using the method described above. The data for the synchronous group are much less self-consistent than those for Sotavalta's

(1952) asynchronous series. However, they seem in general to show that, from the point of view of oscillator theory, there is little difference between the two types.

The slope $K'b_0r^2$ should be related to some other characteristic of the insect, most probably to its weight. For if r is proportional to the wing length l , and l to b_0 , then $K'b_0r^2$ is proportional to the weight of the wing muscle, M_m . It is reasonable to expect that M_m is proportional to the weight of the insect, M_i . In figure 2, the slopes $K'b_0r^2$ are plotted against the corresponding insect weights given by Sotavalta (1952 and 1954). It is apparent that at least for the asynchronous group the correlation is good even though the insects studied cover a wide variety of genera with weights varying from ten to nearly 1000 milligrams.

From figure 3, it appears that the internal moment of inertia, I_{int} , is related to the weight of the wing, M_w . I_{int} is clearly not related to the weight of the muscle M_m , since there is no close correlation between I_{int} and $K'b_0r^2$. Doubtless some portion of the internal and external insect skeleton oscillates with the muscle, and for some not readily apparent reason the inertia of this entire internal structure appears to be

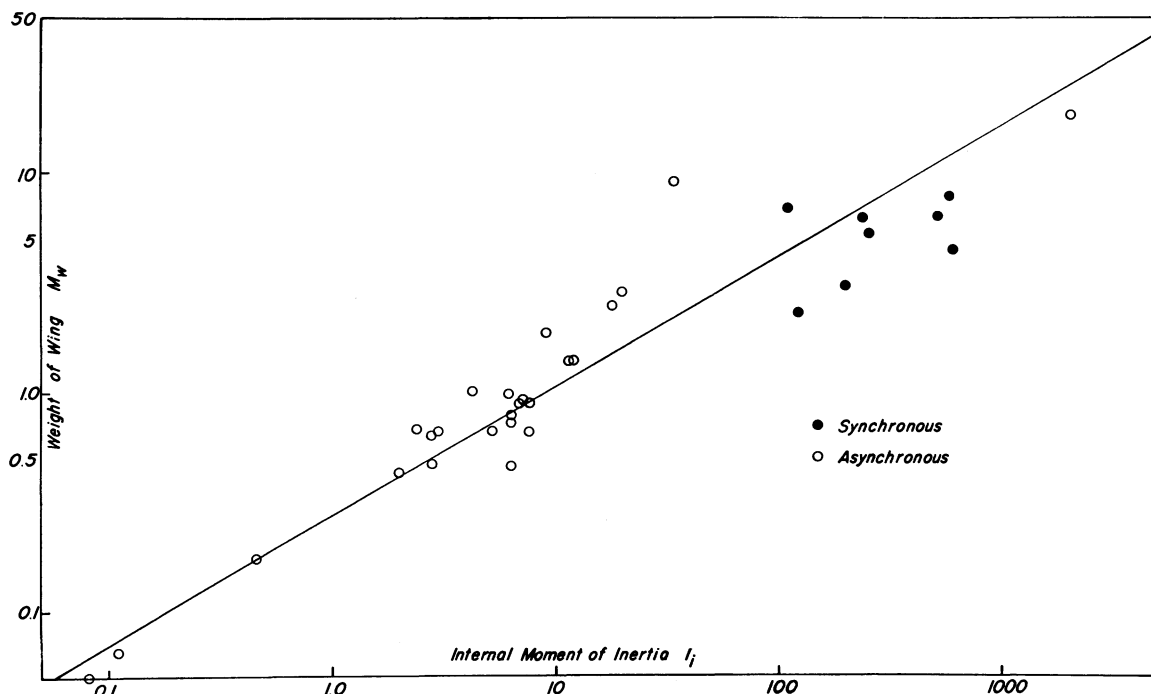


FIG. 3. If we take M_w proportional to l^3 and I_{int} to l^5 , then M_w should be proportional to $I_i^{0.6}$. The slope of the line in the figure assumes the relationship.

more nearly related to the weight of the wing of the insect than to its body weight.

Perhaps one caveat should be introduced here—that the resonance frequency can be maintained only so long as the damping or loading does not exceed the driving capacity of the muscle. This condition is likely to obtain while the insect or bird leads its natural life. When wing loads are applied artificially, such as was done for insects by Sotavalta (1952) and others, the damping may be too large to be overcome by the muscle drive. The amplitude, Φ , of the driven system, eq. (1), under steady-state conditions is given by eq. (6). As B increases, Φ can be held at its appropriate value for a given flight regime and ω at ω_0 for maximum economy in energy consumption, so long as muscle chemistry can increase F_0 correspondingly. However, when F_0 can no longer keep pace with increasing B , as may happen when artificial loads are applied, Φ and also ω may change to the point that free flight becomes impossible.

When aerodynamic requirements for steady flight are such that $B\dot{\phi}$ decreases, maximum economy dictates a decrease in the amplitude Φ . One observes this condition for large birds in cruising flight. Pelicans, for example, flying close to the water appear almost to glide, i.e., the amplitude Φ decreases to a very small value. Should they change course or go into a rapid climb, the amplitude increases markedly. The wing frequency, however, remains constant.

One frequently observes an increase in wing frequency for large birds under unusual and strenuous flight conditions; a female tropic bird, for example, braking before landing at her nesting burrow or eluding pursuit by a demanding male. For this increase in aerodynamic energy output, F_0 must increase inordinately, since we have not only the increased energy output, but also the superimposed losses due to departure from resonance frequency. Limited observations would indicate that such conditions can be maintained only for brief intervals.

The motion of the wings of "ordinary" birds is more complex than is the case for insects or hummingbirds. For the former the wing is fully extended only during the down beat; during much of the up beat it is folded more or less closely in to the body. Therefore, the moment of inertia is less for the up beat than for the down beat and one would expect a corresponding decrease in the duration of the up beat. For the chickadee, high-speed motion pictures

show this to be the case—the time interval for the down beat is 50 per cent greater than for the up beat. This implies a departure from the simple harmonic motion assumed for the wing beat of insects and hummingbirds. The solutions of eq. (7) for such birds would require knowledge of the time dependence of inertia and damping throughout the entire wing beat for each species considered. Sufficient data are not available even for an approximate solution. The basic principles implicit in the simpler equations would, however, still be valid. The wings of ordinary birds will beat at a resonance frequency, and the consequences of a departure from the resonance condition will be qualitatively similar to the situation for insects and hummingbirds.

It is interesting also to note that the dependence of wing beat rates on the size of dimensionally similar groups of flyers is consistent with eq. (4). Sotavalta in several papers (1947, 1952, 1954) gives wing frequencies and wing lengths for a host of insect species. I have determined wing frequencies and wing lengths for perhaps forty hummingbird species ranging from *Calliphlox amethystina* (male) ($\nu = 80 \text{ sec}^{-1}$) to *Patagona gigas* ($\nu \simeq 10 \text{ sec}^{-1}$), and also for a number of passerines ranging in size from chickadee to mockingbird. Meinertzhagen (1955) gives data for a number of large birds whose wing frequencies were sufficiently low to permit visual counting. The literature, unfortunately, gives very little additional data on wing frequencies of birds, particularly those of small or intermediate size.

Figure 4 shows all of these data plotted against wing lengths in logarithmic coordinates. One sees that the points appear to be bounded by a straight line described by the empirical relation

$$\nu l^{1.15} = \text{constant}. \quad (9)$$

In figure 4, wing length is the distance from wing tip to the first articulated joint. For insects and hummingbirds, this is the whole length of the wing since the first articulated joint is at the shoulder. For birds, the first joint is at the wrist, and the length as given is about 60 per cent of the length of the fully extended wing. The measurements for birds join smoothly with those for insects, presumably because the length from tip to wrist for ordinary birds happens to be roughly equal to the effective average wing length during flight.

The detailed relationships between l , b_0 , r ,

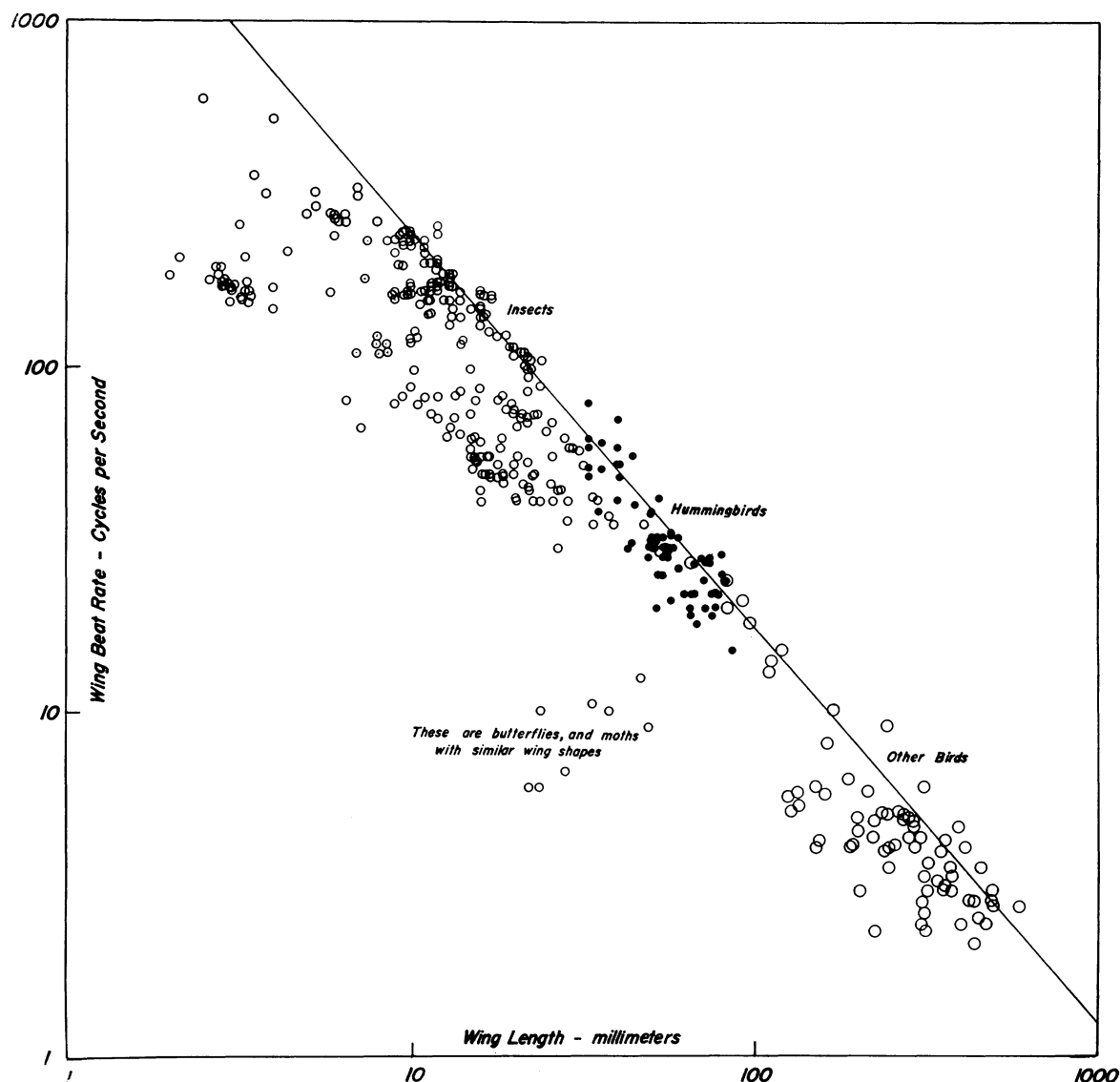


FIG. 4. Wing beat rate and wing length for insects, hummingbirds, and other birds.
The equation of the boundary line is $\nu l^{1.15} = 3540$.

and I depend on the anatomy of a particular family of birds or insects. Yet one would expect that b and r are roughly proportional to l , I proportional to l^5 , and M_i to l^3 . For such a series of animals eq. (4) predicts

$$\nu l = \text{constant}. \quad (10)$$

For insects, such relationships appear to hold. When we group Sotavalta's data into insect families which are more or less dimensionally similar, we find groups of straight lines which agree with eq. (10), each line terminating ap-

proximately at the boundary line given by eq. (9).

For hummingbirds the anatomical relationships appear quite different. Here we find the weight of the bird proportional to $l^{1.5}$, not l^3 . Taking r proportional to l , and b_0 to $M^{1/3}$, hence to $l^{0.5}$, we find $\nu l^{1.25} = \text{constant}$.

For birds, A. Magnan (1922) gives data on wing length, wing area, and wing weight for several hundred species whose body weight ranges from 4 grams to nearly 10 kilograms. Sotavalta gives similar data for perhaps sixty

insect species whose body weights range down to a few milligrams. When wing lengths and wing areas for this array of flying animals are plotted in logarithmic coordinates one finds a slope of 2, indicating, as would be expected, that wing area is proportional to l^2 . However, when wing weights are plotted against wing area, the data fall on a continuous straight line with slope 1.65—not 1.5, as might have been expected. This implies a variation in wing thickness with $l^{1.3}$, in accord with the empirical boundary relation of eq. (9). Perhaps Nature increases the relative thickness of the wing to limit flexing at the wing tip under conditions of normal flight.

In any event the boundary relation per se is not founded in oscillator theory but is in all probability related to aerodynamic efficiency with Nature making small changes in her "model" as the flying animal increases in size to conform to sound and efficient principles of avian design.

It is unfortunate that the ornithological literature is so devoid of wing frequency measurements. It is to be hoped that another Magnan will emerge who will fill this gap in our knowledge of birds as thoroughly and as convincingly as Sotavalta has performed the task for insects.

In summary, the wing beat rates of all insects and hummingbirds studied, and probably of most birds, can be fully explained by the theory of mechanical oscillators. Within dimensionally similar families the frequencies vary with the size of flyer, in accordance with the equation

$\nu^n = \text{constant}$, as expected from this theory. The value of n depends on the dimensional relationships for the family, and appears to fall within the limits 1.0 to 1.25. For all birds and insects there appears to be a limiting boundary for which $\nu^{1.15} \simeq 3540$, where ν is full wing beats per second and l is in millimeters.

There is, of course, no inherent relationship between wing frequencies, as regulated by oscillator theory, and flight techniques or flight efficiencies. Oscillator theory per se relates only to wing beat rate and gives no clues as to how the beating wings produce lift or propulsion.

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