THE FLIGHT MECHANISM OF SWIFTS AND HUMMINGBIRDS

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DESPITE the considerable lapse of time since Westover (1932) showed by cinephotography that the Chimney Swift, *Chaetura pelagica*, beats its wings in unison, the illogical supposition that it may beat them alternately tends to persist. Aymar (1938) seemed frankly skeptical of the photographic evidence. Even Peterson (1947), although granting the evidence, tempered the term illusion by "at least." Recently, Storer (1948) included photographs showing synchronous beats, but said that "at times the chimney swift seems to beat its wings alternately, at other times simultaneously," leaving the reader in some doubt as to whether he considered the alternate wing beat illusory or real.

Several years ago, although it was realized that flight with alternating beats was a virtual impossibility because in a uniform medium the bird's body would oscillate strongly about its longitudinal and vertical axes, I watched Chimney Swifts stroboscopically in order to secure further evidence. A simple, clockwork, rotating shutter was arranged to cover the right objective of a pair of binoculars. By watching birds in direct flight toward or away from me and by closing the left eye, it was often possible with some practice to "stop" the wings for two or three beats, which was ample to show that they moved in unison. Actually, after about two months of almost daily observation, it was found that an increased ability to analyze motion allowed all but the most complex evolutions to be followed without the stroboscope. There is no doubt that the Chimney Swift, like all other birds, may stall one wing in a short turn and may use beats of unequal strength in various manoeuvers; but I could see not the slightest suggestion that in normal flight it ever uses anything approaching an alternate beat.

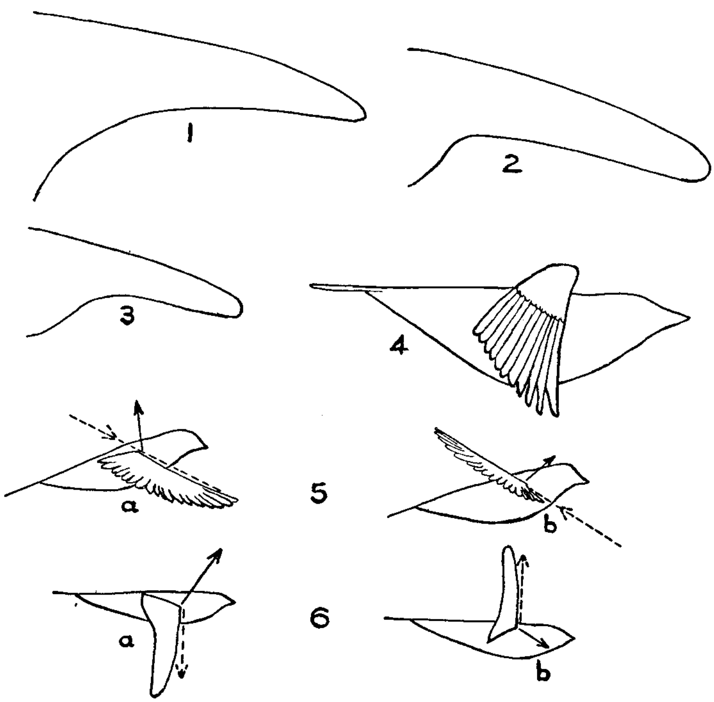
The illusion seems to be explainable largely upon the following facts. The wings of the Chimney Swift are heavily pigmented and are thus somewhat more readily visible in motion than those of many birds of comparable size. They beat just slowly enough to be observed with some difficulty; if they beat half as fast their motion would be obvious, if twice as fast they would be invisible. All who have watched the Nighthawk, *Chordeiles minor*, will recollect the manoeuver by which it takes an insect that is just off its line of flight. If the insect is to its left it banks to the left, swings in that direction and then, after the strike, usually banks and turns back to its original course. The

Chimney Swift does this same trick very frequently, but does it much faster because of its small size and weight. Thus the observer sees the wings stilled for a fraction of a second, one up and one down, and then, after a beat or two, the reverse. I believe that misinterpretation of this action which, although fast, is much slower than the wing beats is responsible for many of the claims of alternate beats.

Perhaps the illusion has been fostered also by the feeling that there must be something unusual about the flight of the swifts as a group to account for their proverbial speed. It may, therefore, be profitable, if only to aid in laying the bogey, to inquire into their flight mechanism. To do so it will be helpful if we consider the swifts with the related hummingbirds whose speed of flight is not merely an illusion engendered by their small size.

First it must be emphasized that both the Ruby-throated Hummingbird, *Archilochus colubris*, and the Chimney Swift, which will be used as examples of the two families, possess in high degree what may be termed the high-speed wing; it is thus almost inevitable that they should be fast fliers. The general characteristics of this wing (Fig. 1) are: pronounced sweepback of the leading edge and sometimes also of the trailing edge; gradual taper to an elliptical tip; relatively slight camber; and a conspicuous fairing at the junction of the trailing edge with the body. In much the same outward form, but with considerable structural differences, this type of wing has been independently evolved in several groups of birds including the ducks, falcons, plovers and sandpipers, swifts and hummingbirds, and swallows. Figure 1 approximately represents the wing of the Golden Plover, *Pluvialis dominica*, and will serve as a typical, well developed, high-speed wing. Figures 2 and 3, which are not to scale, show the wing plans of the Chimney Swift and the Ruby-throated Hummingbird. The sweepback is pronounced and each wing possesses a large fairing of rather unusual form. The only conspicuous difference between them is that the hummingbird's wing is disproportionately short, which is to be expected in a very small bird. Thus both birds have the form of wing demanded by fast flight, and the wings possess further peculiarities that emphasize the birds' relationship.

There is reason to believe that in most birds in level flight the wing is "feathered" (in the oarsman's sense) during the up-stroke; that is to say, the stroke is more or less neutral, producing the minimum of thrust or drag. This effect is achieved in several ways: 1) the wing is partly folded by bending backward and slightly downward at the wrist to reduce its area; 2) the webs of the primaries separate from each other to allow the passage of air; 3) the camber of the wing comes into play; and 4) the wing is raised with the leading edge highest so that the air stream and the elevating muscles tend to combine in raising it (Fig. 4). That little power is exerted on the up-stroke in many birds is indicated by the relatively small size of the elevating muscles. Thus the elevating muscles of an American Robin, *Turdus migratorius*, weighed little more than a tenth as much as the depressing muscles and only 1.6 per cent of the weight of the bird (Table 1). In contrast, the elevating muscles of the Ruby-throated Hummingbird are relatively enormous, nearly one-half the weight of the depressing muscles which are also large. In hovering, the up-stroke (now directed largely backward) must do work. The down-stroke, with its pronounced forward element, inevitably supplies some backward thrust with the lift, and the up-stroke supplies a counterbalancing



FIGURES 1–6 (not to scale).—1) Plan view of typical high-speed wing; 2) Plan view of wing of Chimney Swift; 3) Plan view of wing of Ruby-throated Hummingbird; 4) Typical, neutral up-stroke, probably used in most birds other than swifts and hummingbirds; 5) Wing-action in hovering: (a) down-stroke, (b) up-stroke. Broken arrows show direction of wing movement; solid arrows show approximate size and direction of resultant force acting on bird; 6) Probable wing-action of swifts and hummingbirds in level flight: (a) down-stroke, (b) up-stroke. Symbols as in Figure 5.

forward thrust together with additional lift (Fig. 5). Moreover, there is no appreciable air stream to aid the up-stroke.

If a bird uses a powered up-stroke in level flight, the down-stroke will supply forward thrust and the lift necessary to maintain altitude, whereas the up-stroke will supply only forward thrust (together with some inevitable negative lift, which must be counted as a loss). Such action is shown in Figure 6. For the two strokes to supply equal thrust it is plain that the up-stroke need not consume nearly as much power as the down-stroke. If the hummingbird utilizes its elevating muscles as fully in level flight as in hovering, it may well be that the up-stroke supplies nearly as much forward thrust (not total power) as the down-stroke. For such a mechanism to be effective the wing must not have its flight feathers separated and must not bend at the wrist, as described earlier, but must remain relatively rigid. Further-

TABLE 1

WEIGHTS OF BREAST MUSCLES OF AMERICAN ROBIN AND RUBY-THROATED HUMMINGBIRD

	American Robin			Ruby-throated Hummingbird		
	Total weight	*Depressor muscles*	*Elevator muscles*	*Total weight*	*Depressor muscles*	*Elevator muscles*
Weight (grams)	72.5	10.01	1.15	2.49*	0.51	0.23
Percent of total	100	13.90	1.60	100	20.50	9.25

* Weight after dissection, 30 hrs. after death. Weight at death was 2.93 grams.

more, the wing must not be strongly cambered, for it would then be negatively cambered and proportionately inefficient on the up-stroke. Examination of the wing of the Ruby-throated Hummingbird shows that both the shafts and the webs of the primaries are surprisingly rigid for their size and that there is little tendency for the feathers to separate under pressure on the upper surface. It may also be noted at this point that any tendency for the primaries to separate is greatly lessened if the wing is not bent at the wrist. As already noted the hummingbird wing has little camber, and it may be regarded as eminently suited for flight with a powered up-stroke. The aerodynamic efficiency of the wing must certainly be somewhat lower on the up-stroke than on the down-stroke, but there is no known method of calculating it. It should be emphasized that wind-tunnel tests in which the wing is treated as a rigid airfoil give so untrue a picture of the performance of a bird wing as to be virtually useless. We can only guess what proportion of the thrust can be supplied by a powered up-stroke, but it may well be over 25 per cent.

Now let us consider the Chimney Swift in the light of this proposed flight mechanism. As in the hummingbird, the shafts and webs of the outer primaries are relatively stiff. Some further stiffening is provided by the marked backward curve of the distal parts of the shafts of the three outermost primaries, which tends to keep all the outer shafts close together.

The weak part of a wing that is to be held rigid on the up-stroke is the wrist. At first glance this fact might be considered an argument against a powered up-stroke in the Chimney Swift, for the arm bones are very short, which brings the wrist in toward the base of the wing and the bending moment on it (considering the wing as a uniformly loaded cantilever) is thus considerably increased. If the Chimney Swift's wing is compared with the superficially similar one of the Tree Swallow, *Iridoprocne bicolor*, which has nearly the same overall length, it will be found that the upper arm and the forearm of the swift are roughly half the length of the swallow's, whereas the hand is slightly longer. Further consideration shows, however, that humerus, radius, and ulna are remarkably heavy in the swift, that the elbow is capable of very little movement, and that the wrist, although sufficiently flexible horizontally to allow folding of the wing when the bird is at rest, is massive and very rigid vertically. A heavy sheet of tendon runs over the forearm and over the top and front of the wrist and attaches to the hand. Tendons so situated are not by any means confined to the swifts, but in the Chimney Swift they are much more robust than in other small birds that I have examined. The amount that a tendon will stretch under a given load is clearly proportional to its length. The shorter the arm bones, and consequently the tendons, the less will be the sagging of the wing on the up-stroke, for the power will be transmitted to the hand largely through these tendons. It appears that the swift's wing will be locked rigidly at the wrist on the up-stroke and that its peculiar structure may have evolved because of its value in this mode of flight.

In point of fact, few will deny the comparative rigidity of a swift's wings in flight. It is this rigidity, in contrast with the fluidity of a swallow's wing beats, that cause the swift's flight to be labelled as jerky or flickering. How much power may be applied in the up-stroke is a matter of conjecture. I do not have available the weights of the breast muscles of the Chimney Swift, but the conspicuously large keel in this species, and in the family generally, provides ample room for the attachment of large elevating muscles such as are found in the Ruby-throated Hummingbird.

It is my opinion that the flight mechanism of both swifts and hummingbirds involves a powered up-stroke, which is an appreciable factor in their speed of flight.

SUMMARY

A stroboscope supplied further evidence that the wing beats of the Chimney Swift are always synchronous, never alternate. The illusion of alternate beats is partly due to the bird banking alternately to right and left, as it veers in pursuit of an insect, and then resumes its course. The flight mechanism of the swifts and hummingbirds is suggested as utilizing a powered up-stroke, supporting evidence being drawn from the large elevating muscles, the wing structure and the appearance in flight.

LITERATURE CITED

AYMAR, G. C. 1938. Bird Flight. (Garden City Publ. Co., New York).

PETERSON, R. T. 1947. A Field Guide to the Birds. (Houghton Mifflin Co., Boston), 2nd. Ed.

STORER, J. H. 1948. The Flight of Birds. (Cranbrook Inst. Sci., Bloomfield Hills).

WESTOVER, M. F. 1932. The flight of the swifts. Bird-Lore, 34: 253–254.

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