MORE DATA ON THE WING FLAPPING RATES OF BIRDS

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The present article is an extension and partly a revision of a recent note (Blake, Auk, 64, 1947:619-620) dealing with the wing-flapping rates of birds. I have acquired nearly 500 new observations of which about one-third have been incorporated in a separate paper on the flight of swallows (Blake, Auk, 65, 1948:54-62). Special attention was given to so describing each observation as it was made that it could be assigned to a style of flight. The methods employed, using a stop watch, are the same as those of the first paper referred to and, as in previous papers, the measure of variation used is the standard deviation (σ). It must be admitted that the standard deviation is not a perfectly correct measure of the variation since the distribution of rates for any bird and any style of flight is obviously curtate at both ends, but in most cases the curtation is not so severe as to affect very greatly the validity of the standard deviation.

Gavia immer. Common Loon. 2.8 complete flaps per second; one observation.

Pelecanus occidentalis thagus. Brown Pelican. 2.3-2.5. This and the two following are cited from Coker (Proc. U. S. Nat. Mus., 56, 1919:449-511).

Sula variegata. Peruvian Booby. 2.7-2.8.

Phalacrocorax gaimardi. Red-footed Shag. 4.2-5.0. The rate is much higher than that of the North American *P. auritus auritus*.

Ardea herodias herodias. Great Blue Heron. 2.1; 4 observations. This is the slowest average I have found for any species and it appears to be close to the minimum possible for steady flapping flight.

Butorides virescens virescens. Green Heron. 2.8; 4 observations. In another case the bird had just been flushed and was evidently hurried; the rate was then 3.8 per second.

Nycticorax nycticorax hoactli. Black-crowned Night Heron. 2.6 σ 0.27; 18 observations. Despite the quite reasonable value of the standard deviation and the lack of contrary evidence from the circumstances noted at each observation I am not entirely satisfied that only one style of flight is represented. The span of the rates is low: 2.1 to 3.0 but there is a hint of bimodality at 2.3 and 2.8.

Botaurus lentiginosus. American Bittern. 3.3; 1 observation. The bird passed close to me and may have been hurried: The wing strokes were noticeably shallow.

Branta canadensis canadensis. Canada Goose. 2.6; 1 observation of low-flying birds.

Anas rubripes. Black Duck. The still insufficient data simply show that the flight of this species is quite variable. The rate for long flights at some altitude is about 2.7 per second. A bird flying low with shallow strokes in a moderate wind showed 5.0 per second.

Buteo jamaicensis borealis. Red-tailed Hawk. 2.6; 1 observation of not quite steady flapping.

Pandion haliaetus carolinensis. Osprey. 2.6; 1 observation of hovering in a light wind.

Falco sparverius sparverius. A little more data shows marked variations in wing rate. In still air the rate is about 2.8 but an observation of a bird flying against a moderate wind shows 4.6.

Charadrius semipalmatus. Semipalmated Plover. 5.6; 1 observation soon after flushing.

Squatarola squatarola. Black-bellied Plover. 3.4; 1 observation of a bird at considerable height.

Crocethia alba. Sanderling. 6.3; 1 observation, the bird flying across a moderate wind.

Larus marinus. Great Black-backed Gull. 2.4 σ 0.35; 6 observations. I suspect that this species really has a very slightly slower rate than the Herring Gull.

Larus argentatus argentatus. Herring Gull. 2.5 σ 0.33; 83 observations. The span of these observations is from 1.8 to 3.3 per second. I have had no success in finding significantly different classes within this array. The most likely lead is to compare the wing rates with, against, and across moderate or strong winds. (See the next species.) The Herring Gull gives a few quick flaps just as it lands. One observation of these yielded a rate of 4.0 per second.

Larus atricilla. Laughing Gull. 3.0 σ 0.29; 95 observations. The spread here is from 2.3 to 3.6. The difference between this species and the preceding is just significant. The strength of the wind makes little or no difference in the rate, if we lump all directions relative to the wind; there is the merest hint that the rate across a strong wind is greater than the rate against the same wind. A single observation of a Laughing Gull chasing a tern showed a rate of 4.0 per second.

The best statement that can be now made about gulls is that the rate of flapping probably is related to the angle between wind and flight but that the variation is very small. Present information suggests a maximum average difference of one- or two-tenths of a stroke per second. The rate is least upwind and greatest downwind.

	Up	Across	Down
Herring Gull	2.9 σ 0.09 (5)	2.8 σ 0.15 (7)	3.0 σ 0.53 (9)
Laughing Gull	3.0 σ 0.27 (17)	3.2 σ 0.31 (16)	3.2 σ 0.36 (5)

The data in the above table were accumulated at a favorable point within about two hours during which the wind was sensibly steady as to force and direction. The flights selected for timing were as nearly as possible in the three given directions. No other selection was involved. The numbers of observations are given in parentheses.

The final and least measurable element is the effect of varying urgency of the gull's business on the flapping rate. I have not been able to gather any useful data on this item.

Sterna hirundo hirundo. Common Tern. 3.0 σ 0.27; 17 observations.

Sterna antillarum antillarum. Least Tern. 3.7 σ 0.37; 12 observations. The flapping rate of the Least Tern is a little more uniform than that of the Herring and Laughing gulls. About a quarter of the standard deviation is contributed by one aberrant observation. Two observations of hovering for a dive average 5.3 per second.

Columba livia. Domestic Pigeon. The flight of this pigeon offers difficulties in interpretation. These are, in part, due to difficulties of observations. Pigeons prefer cities; their flights are short, curving, variable as to level, and prone to acceleration and deceleration. Considerable observation leads me to conclude that the species does not have definite styles of flight but rather that rate and amplitude of the wingbeat vary widely but continuously. Nineteen observations of flight which appeared level and uniform give an average of 3.1 σ 0.46. The range is 1.9 to 3.6 and the most frequent rates are 3.3 and 3.6. Four observations of climbing vary from 3.3 to 5.5, with an average of 4.1. These greatly overlap apparently level flight.

Zenaidura macroura carolinensis. Mourning Dove. 3.2 σ 0.58; 7 observations. The flight of this species shows the same type of variability as that of the domestic pigeon. The range of the above observations is 2.2 to 3.8. One observation of a slow climb is 4.5 and another of steeper climbing is 6.4.

Coccyzus erythropthalmus. Black-billed Cuckoo. 3.3; 2 observations of the same bird.

Chordeiles minor minor. Nighthawk. 2.3 σ 0.14; 6 observations. These represent the steady coursing of the Nighthawk. There are two other styles of flight: a flurry of rapid strokes which have a rate in excess of 3.3 and the rather sharp climb which precedes the "boom." The inherent error in the method of observation averages 0.1 stroke per second and hence very little actual variation in coursing is shown.

Chaetura pelagica. Chimney Swift. 5.0 σ 0.3; 7 observations. The Chimney Swift seems to have but one style and rate. The span of the seven observations is from 4.5 to 5.5. The inherent error amounts to 0.5 strokes per second, so no real variation in rate has been observed.

Megaceryle alcyon alcyon. Belted Kingfisher. I have already (Blake, 1947, *op. cit.*: 620) given a figure for the style of flight which consists of a few rapid strokes and a brief glide. There is also a regular flap and glide style. Four observations yield an average of 2.4 per second for this latter style. The rate is the same as for the first style.

Tyrannus tyrannus. Eastern Kingbird. 6.2; 1 observation of a short scaling flight.

Corvus brachyrhynchos brachyrhynchos. American Crow. The flight of crows shows a rather continuous variation from fairly rapid steady flapping to an exaggeratedly slow flap and glide. It certainly does not fall into the quite distinct styles I have previously described for the Blue Jay. Unlike the latter species crows have a marked tendency to sail, and the transition from flap and glide to sailing is represented by an observation of regularly spaced, very shallow flaps between short glides timed at half a flap per second. I have chosen here to separate the observations on the crow into two classes, flapping during level flight where 50 observations average 2.2 σ 0.3 flaps per second and climbing where 11 observations yield 2.7 σ 0.2. There is, of course, considerable overlap of rates with level flight varying from 1.4 to 2.8 and climbing from 2.4 to 3.1. It does not seem useful to attempt a direct comparison with the rates for the Blue Jay since we cannot define discreet styles of flight comparable with those of the jay.

Turdus migratorius. Robin. It now appears that my previous figure for this species (Blake, 1947, *op. cit.*: 620) applies to flap and glide flight which style I had not recognized when the observations were made. A subsequent observation of 2.5 flaps per second is recorded as flap and glide. In contrast, five observations of steady flight yield an average of 4.3 σ 0.54.

Sturnus vulgaris. Starling. I have already given a figure for the usual Starling flight in which the strokes are in groups of three. This bird also has a steady flapping flight. Two observations of it are 5.0 and 6.3 strokes per second, average 5.65.

Agelaius phoeniceus phoeniceus. Red-winged Blackbird. The Red-wing displays four styles of flight which are somewhat intergrading, namely, flap and glide, grouped strokes, steady flapping, and hovering. Intergradation is particularly shown between steady flapping and grouped stroke flight. Rates are as follows: flap and glide, 2.9 per second, 1 observation; grouped strokes, 4.0 σ 0.6, 5 observations; steady flapping, 5.8 σ 0.31, 6 observations; hovering, 4.3, 2 observations.

The low rate for hovering as compared with steady flapping is the same situation as that which was less clearly seen in the flapping rates of the Ruby-throated Hummingbird (Blake, New England Nat. No. 3, 1939:2). The Red-wing is one of the birds that hovers by flying vertically upward at a speed just balancing the fall due to gravity but without any large forward (horizontal) component requiring braking by the tail. Since the net air speed is zero or almost zero, there is no form drag due to the head, body, and tail to overcome and the flapping rate needs only to be great enough to provide lift. Flap and glide or grouped stroke flight can provide both the necessary lift and the power for horizontal velocity at still lower wing rates.

Icterus galbula. Baltimore Oriole. Flap and glide, 2.1 strokes per second; 1 observation.

Quiscalus quiscula aeneus. Bronzed Grackle. This species resembles the Red-wing in having a steady flapping used on short flights and a grouped stroke style used on longer flights. The former shows 4.2 σ 0.66 strokes per second (six observations) and one observation of the latter is 3.1. Both are markedly slower than the Red-wing's performance. A single observation of a Bronzed Grackle climbing just after takeoff is 6.2.

Spinus tristis tristis. Eastern Goldfinch. The data in my earlier paper are not satisfactory. Two new observations of the usual undulating flight average only 2.7 as against 4.7 for two earlier ones. I am not certain that it is safe to count three strokes between each two glides.

In conclusion, I again, as in my first paper, bring forward the teleological aspects of bird flight. As already hinted, the urgency of a bird's business does vary. A small band of crows takes off to fly some distance and it is easy to observe that the hinder birds flap faster than the lead birds, until all the birds are well bunched, when their flapping rates become nearly uniform.

The dependence of power output on wing rate is shown by the increased rate of climbing birds. This has been most clearly observed in the pigeons and the Mourning Dove. A bird, however, differs in several important respects from either a powered airplane or a glider. One of these respects is its ability to alter the attack angle of the wings and hence the lift obtained in gliding. At the same time the drag of the wings may be changed by their flexion or extension,

It would appear that both of these methods are used by the Blue Jay in flap and glide flight. At the beginning of the glide the jay slightly flexes the wings, decreasing the drag and also losing some lift. However, it also loses altitude and the net result is a gain in speed and momentum with little or no output of energy. At the end of the glide the wings are extended, increasing both lift and drag, but particularly the former. Speed is rapidly lost as the momentum is expended, with a compensating gain of altitude. The bird now by a single flap restores the speed to that normal for the beginning of the glide, which immediately follows. It is evident that distance is covered with a relatively low expenditure of energy although at some sacrifice of speed. The jay appears quite conscious of its ground speed and rarely, or never, uses the flap and glide style upwind.

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