FLIGHT SPEEDS AND WINGBEAT FREQUENCIES OF THE MAGNIFICENT FRIGATEBIRD

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FRIGATEBIRDS are well specialized for remaining airborne for long periods of time. Unfortunately relatively little is actually known about their flight capabilities. The Magnificent Frigatebird (*Fregata magnificens*) is primarily a New World species and is seen regularly along the southern coasts of the United States. In the Dry Tortugas, westernmost of the Florida Keys, they often roost in mangroves on Bush Key and on pilings on Garden Key, particularly during the warmer months; they can regularly be observed in flight in the vicinity of these roosts. Harrington et al. (1972) examined the effect of wind on frigatebird flight activities in the Tortugas and compared results with those obtained near another roost on Tarpon Key at the mouth of Tampa Bay, Florida. During the summer of 1967 I visited the Dry Tortugas and gathered information on wingbeat frequencies of Magnificent Frigatebirds and the effect of wind speed on their flight speeds.

STUDY AREA AND METHODS

The Dry Tortugas are described in detail by Robertson (1964). I recorded flight data from Garden Key on 3, 4, and 9 to 12 June 1967. On the first three dates I was positioned near the abandoned coaling docks on the northeastern edge of Garden Key when the wind was still. For the remaining dates and wind conditions, I collected data from the top of the southern wall of Fort Jefferson (34 feet above ground level) which occupies most of Garden Key (see Robertson 1964).

Flight speeds were recorded using an FTB-X(1) Doppler radar described by Lanyon (1962) and Schnell (1965), which consists of five basic elements: (1) a transmitter providing ½ watt of microwave energy at 9,600 megacycles per second; (2) a transmitting antenna; (3) a receiving antenna to collect energy reflected back from a target; (4) a mixer to merge reflected energy with a small sample of transmitted energy; and (5) a receiver to amplify and measure the mixer's audible output, the Doppler frequency. The battery-powered unit is coupled with a tape recorder to record Doppler frequencies and voice commentary. Speeds were measured of birds 40 to 120 yards from the unit, and wind speeds were obtained with a hand-held Bacharach style 3035A anemometer about every ½ hour. Two persons operated the radar—one sighted the unit on a bird and the other read the speed meter and recorded data into the tape recorder. I included a "C" tone of a pitch pipe at the beginning of each tape as a standard to ensure the accurate, later interpretation of Doppler frequencies. Tape-recorded Doppler frequencies were analyzed with a Kay Sona-Graph (model 7029A) to determine wingbeat frequencies.

Spectrograms were made from tape sections recorded of birds in flapping flight (Figure 1). From these diagrams, I determined the time necessary to

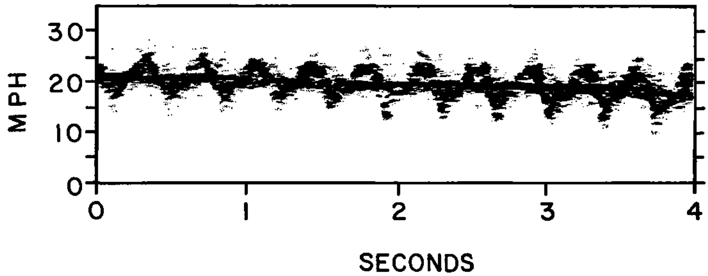

Figure 1. Spectrogram of Doppler frequencies from a Magnificent Frigatebird in flapping flight. At the beginning of the sequence, the bird was flying about 22 mph, after which its speed decreased gradually. While it is not known exactly which parts of the bird are involved in reflecting the transmitted signals that indicate changes in speed, a complete wingbeat corresponds to a single cycle on the graph.

complete two or more wingbeat cycles (segments measured were from 2 to 22 wingbeat cycles long; mean of 7.5 and standard deviation of 5.4), and results were converted into wingbeats per second. Although my recordings were often of only short duration, the birds recorded were usually engaged in extended flapping flight.

I recorded flight speeds from individuals that were not perceptibly gaining or losing altitude. If a bird's flight path was not parallel to the transmitted radar beam the angle between the beam and the bird's path was determined using a scale on the tripod mount, and the recorded speed was corrected appropriately. All recordings were made with a deviant angle between 0 and 20 degrees—angles for which there is little difference between the indicated and true speed. On windy days I divided speeds into three groups: birds flying across the wind, with the wind, and into the wind. The "with the wind" category included those flying directly with the wind or at an angle of less than 45 degrees to this course. Birds flying at an angle of less than 45 degrees to a course directly into the wind were placed in another category, and the remaining birds were considered to be flying across the wind.

I did not differentiate between sexes or by age when recording flight data. There were about 175 frigatebirds in the area. On 12 June, for example, 160 birds were roosting on the abandoned coaling docks, 120 of which were adult females, 25 adult males, and 15 white-headed immatures (John C. Ogden, pers. comm.). These proportions are very similar to those of censuses in later years by Harrington et al. (1972) and probably accurately reflect the relative numbers of flight speeds I recorded for each sex or age group.

Results

Wingbeat frequencies were determined for 21 frigatebirds when there was no wind. These ranged from 2.61 to 3.21 beats per second, with a mean of 2.844 and a standard deviation of 0.136. Table 1 shows wingbeat frequencies recorded at various flight speeds. The negative correlation

TABLE 1

WINGBEAT FREQUENCIES (BEATS/SEC) IN RELATION TO AIR SPEEDS (MPH) OF 20 FRIGATEBIRDS[1]

Air speed					
18	20	22	24	26	32
2.90	2.97	3.21	2.97	2.79	2.83
	2.93	3.03	2.88	2.61	
	2.91	2.85	2.83		
	2.68	2.84	2.75		
		2.81	2.70		
		2.77			
		2.68			

[1] The speed was not recorded for 1 (2.77 beats/sec) of the original 21 determinations of wingbeat frequency. All observations were made when there was no wind.

of 0.253 between wingbeat frequencies and flight speeds is not statistically significant.

Ground speeds and air speeds are given in Table 2. Air speeds were calculated by adding or substracting the median wind speed appropriately to the recorded ground speed if the birds were flying into or with the wind, respectively. The vector diagram in Figure 2 demonstrates how air speeds were calculated for birds flying across the wind.

DISCUSSION

Greenewalt (1960) indicated that wingbeat rates of all insects, hummingbirds, and probably most other birds could be fully explained by the theory of mechanical oscillators. He concluded that, "for maximum economy in energy expended, the wings of flying insects and birds beat at the characteristic frequency of the undamped system." "The theory presumes a resonance frequency for beating wings which will be main-

TABLE 2

GROUND AND AIR SPEEDS (MPH) OF FRIGATEBIRDS

Wind speed	DBRW[1]	Sample size	Air speed	Ground speed	Range[2]	SD
0	—	33	22.55	22.55	12–34	4.31
6–8	Across	151	23.33	22.25	10–38	5.46
	Into	48	24.63	17.63	10–32	4.73
	With	48	23.17	30.17	14–46	6.60
10	Across	19	30.43	28.74	18–38	5.86
	Into	3	30.67	20.67	10–28	9.45
	With	8	22.75	32.75	30–38	2.60
12–15	Across	34	24.67	20.65	12–32	3.80
	Into	7	29.50	16.00	12–20	2.58
	With	5	16.50	30.00	14–44	10.68

[1] Direction of bird in relation to wind.
[2] Range of ground speeds.

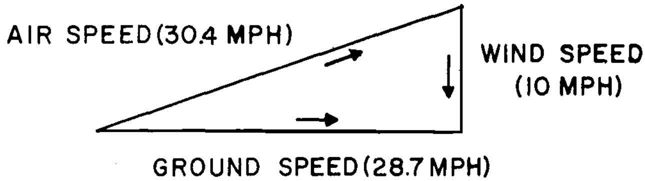

Figure 2. An example of the calculation of air speed for birds flying across the wind.

tained regardless of changes in either external or internal wing loadings" (Greenewalt 1962). It follows that in general the wingbeat rate for a particular animal will be constant, given that its average winglength in flight is not changed. However, birds can and occasionally do exceed their natural frequencies for short periods of time, but at reduced efficiency.

The wingbeat rate of Ruby-throated Hummingbirds (*Archilochus colubris*) remained constant under a great variety of conditions (i.e. in hovering flight, at speeds up to 30 mph, etc.; Greenewalt 1960), and Tucker (1966) reported no relationship between flight speed and wingbeat frequency in the Budgerigar (*Melopsittacus undulatus*). McGahan (1973) found no correspondence between forward air speed and flapping rate for 42 Andean Condors (*Vultur gryphus*) and 5 Turkey Vultures (*Cathartes aura*), although a statistically significant relationship existed between flapping rate and sinking speed. My data on frigatebirds further indicate that wingbeat frequencies in birds are essentially constant within species and are not altered to effect (or as a result of) changes in air speed.

The variation observed in wingbeat rate is probably largely explainable on the basis of size variation in frigatebirds. The coefficient of variation for the wingbeat frequencies I recorded is 4.77%. While I did not obtain morphologic measurements of birds studied in flight, the coefficients of variation for the square roots of wing areas and the cube roots of weights for 10 Magnificent Frigatebirds (5 males and 5 females) measured by Harrington et al. (1972) are 3.15% and 3.58%, respectively. These data indicate that the variation in wingbeat frequency is only slightly greater than predictable on the basis of morphology. Even if additional data on frigatebirds showed the negative correlation of wingbeat frequency with flight speed to be significant, this would not necessarily negate the idea that flapping rates are predictable on the basis of the theory of mechanical oscillators. Rather, it might reflect that the average winglength differs at different flight speeds.

Greenewalt (1960, 1962) plotted wingbeat rates against winglength for many different flying animals. Within dimensionally similar families, flapping frequencies should vary in accordance with the equation

$$\nu\, l^n = \text{constant}$$

where ν is wingbeat frequency in beats per second and l is winglength (i.e. the distace from the wing tip to the first articulated joint, which for most birds is roughly equal to the effective average winglength during flight) in millimeters. The value of n depends on the dimensional relationships of the group being considered. For all birds and insects combined, n is 1.15 in the boundary equation and the constant is approximately 3540 (Greenewalt 1960). The boundary line was drawn such that few animals exhibited higher flapping frequencies than predicted by its equation, although a number had rates that were lower.

Using Palmer's (1962) measurements for Magnificent Frigatebirds, I obtained a weighted average winglength (weighted 120 to 25, females to males, the approximate ratio between the sexes found during my stay on the Tortugas) of 647.1 mm. A flapping rate of 2.07 beats per second is predicted for the Magnificent Frigatebird using the boundary equation, which is substanially lower than the observed mean of 2.84. Only one point for birds on the log-log plot of wingbeat rate against winglength in Greenewalt (1960: Figure 4) deviates this much above the expected flapping rate. It may be that for frigatebirds, which have extremely long primaries relative to other birds of similar size (Palmer 1962), winglength considerably overestimates their effective average winglength during flight—the latter probably being an important parameter in determining the oscillating frequency (Greenewalt 1960).

When there was a wind, most frigatebirds from which I recorded flight speeds used declivity currents and updrafts present above the fort, but some probably utilized thermals. As expected, ground speeds were considerably greater for birds flying with the wind (Table 1). Air speeds were greater for frigatebirds flying into the wind than for those moving across or with the wind. The air speeds are probably slightly underestimated for birds flying into the wind and overestimated for those flying with the wind, because some birds included in these categories were not flying exactly into or with the wind. For these birds the wind effect on their flight was slightly less than the recorded wind speed. I did try to measure flight speeds only for birds that deviated little from a direct course into or with the wind, and the estimated air speeds are probably not substantially in error from this factor.

Tucker and Parrott (1970) examined the strategies for maximizing the distance traveled or altitude gained—two of the possible functions of gliding flight—under various environmental conditions. High air speed is an advantage only when gliding into a head wind while in the process of maximizing the distance traveled. For their simplified model, air speed should be minimized under other conditions to achieve maximum distance or altitude.

It appeared that most birds measured for flight speeds were engaged in static soaring (Cone 1962, 1964). Aerodynamically there is no reason to expect that statically soaring frigatebirds would fly at faster air speeds into the wind than with or across the wind. Further data are needed for Magnificent Frigatebirds and other species that perform static soaring to determine if they do in fact fly into the wind at faster air speeds. Of course, as in this study, one of the most difficult aspects in approaching the problem is differentiating between when a bird is engaged in static soaring and when it is involved in some other type of soaring flight.

Acknowledgments

I wish to thank Austin Osborn for assisting during the field work and Patricia Walker for helping to analyze data. William B. Robertson, Jr., and John C. Ogden also provided various forms of assistance. Crawford H. Greenewalt made a number of valuable suggestions after reading an earlier version of the paper. My work was supported by a grant from the Frank M. Chapman Memorial Fund, and the radar unit was made available through the American Museum of Natural History.

Summary

Wingbeat frequencies and flight speeds of Magnificent Frigatebirds were recorded with a Doppler radar in the Dry Tortugas, Florida. The flapping rate averaged 2.84 beats per second (SD 0.14) and was not significantly correlated with flight speed, providing further evidence that for birds wingbeat frequency is essentially constant within species. The observed flapping rate is somewhat higher than predicted from the theory of mechanical oscillators when the distance from the end of the wing to the first articulated joint is used as an estimate of the average effective winglength.

Flight speeds of birds in a flat calm averaged 22.55 mph. The highest average ground speed of 30.17 mph was obtained from frigatebirds flying with a 6 to 8 mph wind, and the lowest of 16.00 mph for birds flying into 12 to 15 mph wind. Airspeeds were greater for frigatebirds flying into the wind than for those moving across or with the wind.

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