FLIGHT SPEEDS OF BIRDS IN RELATION TO ENERGETICS AND WIND DIRECTIONS

VANCE A. TUCKER AND KLAUS SCHMIDT-KOENIG

RECENTLY it has become possible to measure accurately the power expenditures of birds flying freely in a wind tunnel (Tucker, 1968, 1969). The measurements show that power expenditure is influenced by the air speed and the angle of flight, which may be level, ascending, or descending. As the air speed and angle of flight in a wind tunnel are chosen by the investigator, we were interested in determining if birds flying in natural conditions choose air speeds that minimize their power expenditures.

Accurate measurements of air speed and angle of flight in nature are difficult to make. The velocity vectors of both the bird and the wind must be measured, and then the motion of the bird relative to the air must be determined by vector addition. Both vectors may change in time and space. As the unaided human eye usually is incapable of measuring the distances and angles on which accurate measurements of the velocities must be based, relatively elaborate tracking and recording devices are needed.

Although many estimates of bird flight speeds have been published (Baker, 1922; Cooke, 1937; Cottam et al., 1942; McCabe, 1942; Broun and Goodwin, 1943; Spiers, 1945; Meinertzhagen, 1955; Pearson, 1961; Thompson, 1961; Lanyon, 1962; Schnell, 1965; Lokemoen, 1967; Michener and Walcott, 1967), the accuracy of most of them cannot be evaluated because the descriptions of methodology are incomplete. Most estimates are for ground speed with little or no information on wind velocity. Often the birds were chased by automobiles or aircraft, or were otherwise disturbed, and angles of ascent or descent were not measured.

We measured velocities with respect to air and ground of birds in nature by using a double theodolite system. In this technique, the bird is sighted on through telescopes operated by two observers at different locations. The horizontal angles and one vertical angle of the lines of sight of the telescopes are recorded simultaneously and at known times. The position of the bird in space at each time can be reconstructed from these data so that three-dimensional velocity vectors can be determined. Wind velocity vectors in two dimensions can be measured in a similar manner by tracking helium balloons.

MATERIALS AND METHODS

The theodolites were made from surveyor's transits with horizontal and vertical circles graduated to 5 minutes of arc. A motor-driven 35-mm camera mounted on each transit photographed the readings of the graduated circles through a system of

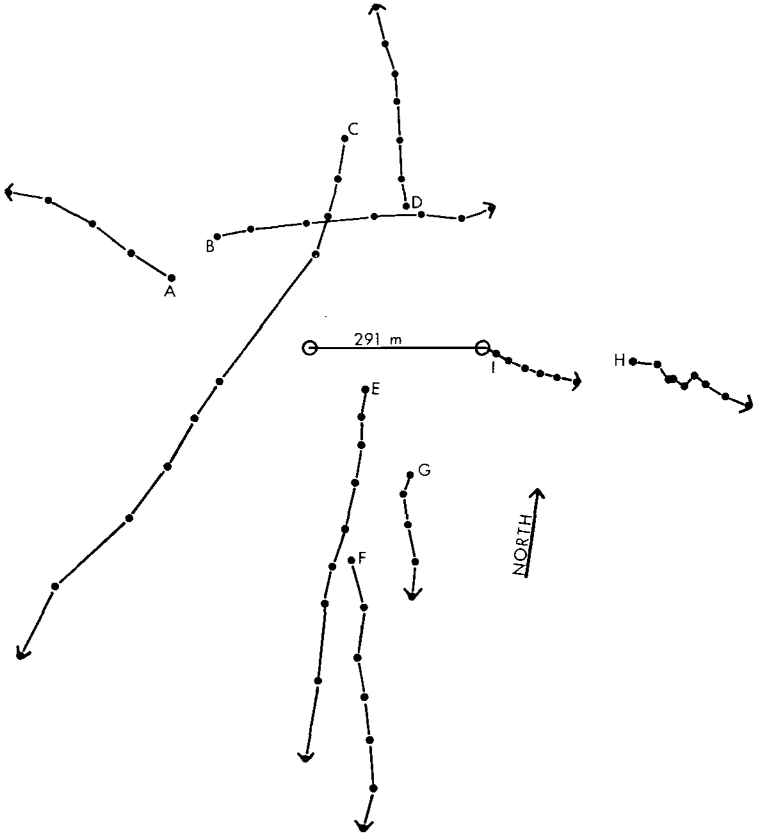

Figure 1. Ground paths of selected birds and of one helium balloon. Dots mark positions determined by theodolites, open circles represent theodolite stations, arrow heads show direction of flight. Most birds flew at altitudes less than 50 m above ground level. A, Common Crow; B, Snowy Egret; C, American Widgeon; D, Laughing Gull; E, Pintail; F, Canada Goose; G, Sparrow Hawk; H, Osprey; I, balloon.

mirrors. The cameras also photographed clock faces that showed time to the nearest 0.1 second. Radio signals controlled the cameras and provided voice communication between the theodolite stations. A button mounted on one theodolite triggered both cameras within 0.003 seconds of one another.

In the field, the theodolites were set up on their tripods and leveled. The horizontal circles were aligned along a baseline by adjusting them while the telescopes were set to sight through one another. We determined the length of baseline between the theodolites by triangulation (Figure 1). The three angles of the triangle were formed between the two theodolites and a stake set out 15.0 m along a line at right angles to the baseline at one theodolite station.

When one of us saw a flying bird, he contacted the other by radio, and both observers indicated when they had the bird in the fields of view of their telescopes. With practice we could locate a bird in the telescopes in a few seconds and could keep the cross hairs in the telescopes within a body length of the bird. Misalignment of the cross hairs causes an error in the calculated position of a bird, the magnitude of which depends on the location of the bird relative to the theodolites. The error is insignificant in the present study for most locations within four baseline lengths of the theodolites. One of us triggered both cameras at various intervals according to the complexity of the bird's flight path and recorded the species and time immediately after the last photographs were taken. Wind velocity at the altitudes where the birds were flying was determined every 1 or 2 hours by tracking helium balloons 0.2 m in diameter.

The velocity vectors of a bird with respect to both the air and the ground were computed from the theodolite records. To avoid confusion, certain terms will be used strictly with the following meanings: Velocity refers to both the magnitude and direction of a vector, while speed refers only to the magnitude of velocity. Air velocity is a three-dimensional vector that describes a bird's motion relative to the air. Ground velocity is a two-dimensional vector that describes the projection on the earth's surface of a bird's motion. Wind velocity is a two-dimensional vector that describes the projection on the earth's surface of the motion of the air.

We made measurements on 24 and 25 September 1967 at Pea Island Waterfowl Refuge on the North Carolina Outer Banks. The theodolites were set up on a narrow, artificial dike about 3 m high that ran east and west across the flat marsh. The relief of the area, including vegetation, was less than 1 m for at least 1 km both up- and downwind. With the exception of a soaring Osprey (*Pandion haliaetus*), all the birds we tracked appeared to be cruising cross-country.

RESULTS

The winds on the days the measurements were made were typical, steady coastal winds. Mean wind speeds, estimated from balloon tracks at the altitudes where birds were flying, were 5.1 m/sec (11 mph) one day and 8.5 m/sec (19 mph) the next. Minimum and maximum wind speeds over an hour were estimated at 65 per cent to 135 per cent of mean wind speed (Giblett, 1932), which corresponds to a standard deviation for wind speed of less than 2 m/sec (4.5 mph).

We made most of our measurements on ducks, gulls, terns, and herons, and a few measurements on other types of birds (Tables 1, 2). For species in the groups mentioned we classified the inclination to horizontal of each air velocity vector in one of five categories: steep descent ($< -5°$), shallow descent ($> -5°, \leq -2°$), level ($> -2°, \leq 2°$), shallow ascent ($> 2°, \leq 5°$), and steep ascent ($> 5°$). Most of the air velocity vectors were shallow descent or ascent, or level (Table 2). Analysis of variance indicated that only in the Little Blue Heron was there a significant change in air speed at different inclinations ($0.995 < P < 0.999$). Probability levels for other species were less than 0.95.

We also classified the direction of each air velocity vector according to whether it was into a headwind (within 45° of the wind source), with a tailwind (within 45° of the wind destination), or with a crosswind (remain-

TABLE 1

AIR SPEEDS OF VARIOUS BIRDS[1]

Bird	No.	Mean air speed, m/sec (SE, N)
American Widgeon (*Mareca americana*)	1	17.7 (0.75, 9)
Black Duck (*Anas rubripes*)	1	17.9 (0.83, 5)
Gadwall (*Anas strepera*)	2	20.7 (0.68, 6)
Pintail (*Anas acuta*)	16	16.6 (0.37, 62)
Unidentified ducks	5	17.4 (0.63, 26)
Herring Gull (*Larus argentatus*)	9	12.6 (0.50, 35)
Laughing Gull (*Larus atricilla*)	3	12.6 (0.72, 14)
Caspian Tern (*Hydroprogne caspia*)	5	11.7 (0.57, 21)
Royal Tern (*Thalasseus maximum*)	4	13.2 (0.42, 18)
Common Egret (*Casmerodius albus*)	2	10.8 (0.50, 6)
Great Blue Heron (*Ardea herodias*)	1	14.3 (0.56, 4)
Little Blue Heron (*Florida caerula*)	3	11.6 (0.56, 15)
Louisiana Heron (*Hydranassa tricolor*)	1	12.4 (0.30, 2)
Snowy Egret (*Leucophoyx thula*)	4	12.0 (0.47, 20)
Sandpipers (*Erolia* spp.)	1	19.1 (0.49, 2)
Black-bellied Plover (*Squatarola squatarola*)	3	16.2 (0.68, 7)
Common Grackle (*Quiscalus quiscula*)	2	17.3 (0.06, 3)
Redwinged Blackbird (*Agelaius phoenicius*)	1	14.1 (2.12, 2)
Canada Goose (*Branta canadensis*)	2	13.9 (0.24, 11)
Common Crow (*Corvus brachyrhynchos*)	3	12.7 (0.35, 12)
Boat-tailed Grackle (*Cassidix mexicanus*)	1	11.9 (0.18, 5)
Sparrow Hawk (*Falco sparverius*)	1	11.1 (0.30, 4)

[1] No., number of individuals or flocks; SE, standard error of mean; N, number of air speed determinations; 1 m/sec = 2.24 mph = 3.60 km/hour.

ing angles). Only four species had air velocities in all three categories (Table 3). Analysis of variance showed that the air speeds of all four species varied significantly ($P < 0.995$) with wind direction.

On one occasion an Osprey was tracked as it soared without flapping from an altitude of 147 m to 199 m in 40 seconds. At the time, the bird appeared to be circling as it moved downwind. Correcting for wind velocity showed that the bird actually was traversing back and forth across a region of air 70 m wide, presumably a thermal, at air speeds between 4 and 7 m/sec (9 and 16 mph). The Osprey's maximum rate of climb was 3.5 m/sec.

DISCUSSION

All our air speed values are within the range of those reported by others. Ducks, shorebirds, and Common Grackles were the fastest birds, with air speeds in excess of 16 m/sec (36 mph). Canada Geese, gulls and terns, and a Redwinged Blackbird flew at about 13 to 14 m/sec (29–31 mph). Herons and other species were slowest, with speeds below 13 m/sec (Table 1).

TABLE 2

AIR SPEEDS OF DUCKS, GULLS, TERNS, AND HERONS DURING LEVEL, ASCENDING, AND DESCENDING FLIGHT[1]

Bird	Mean air speed, m/sec (SD, N), angle of flight (descent –)				
	< -5°	> -5°, ≦ -2°	> -2°, ≦ 2°	> 2°, ≦ 5°	> 5°
American Widgeon	16.6 (–, 1)	–	18.9 (3.09, 3)	17.5 (2.18, 4)	16.3 (–, 1)
Black Duck	–	17.1 (–, 1)	18.3 (2.40, 2)	19.7 (–, 1)	16.1 (–, 1)
Gadwall	–	21.6 (0.66, 3)	19.7 (1.97, 3)	–	–
Pintail	14.4 (3.46, 3)	15.6 (2.24, 12)	17.1 (2.91, 35)	18.6 (2.17, 11)	15.2 (3.49, 6)
Herring Gull	13.4 (–, 1)	10.4 (3.02, 5)	13.7 (3.08, 18)	11.9 (2.47, 7)	11.5 (1.25, 4)
Laughing Gull	–	11.9 (1.18, 5)	15.2 (5.43, 3)	12.3 (0.76, 4)	10.8 (0.14, 2)
Caspian Tern	11.4 (2.95, 3)	12.8 (2.48, 4)	11.0 (3.38, 8)	12.0 (1.62, 6)	–
Royal Tern	–	13.9 (–, 1)	13.4 (2.45, 8)	12.9 (1.77, 3)	13.0 (0.98, 6)
Common Egret	–	10.6 (1.37, 3)	11.0 (1.30, 3)	–	–
Little Blue Heron	–	7.2 (–, 1)	12.6 (1.28, 11)	9.5 (1.67, 3)	–
Snowy Egret	–	10.9 (2.71, 6)	12.5 (1.68, 14)	–	–

---

[1] SD, standard deviation; other symbols as in Table 1.

TABLE 3
AIR SPEEDS OF VARIOUS BIRDS IN WINDS OF DIFFERENT DIRECTIONS[1]

Bird	Air speed, m/sec (SE, N)		
	Headwind	Tailwind	Crosswind
Pintail	18.4 (0.85, 16)	15.5 (0.55, 26)	16.5 (0.39, 20)
Herring Gull	14.9 (0.73, 14)	11.8 (0.46, 11)	10.3 (0.69, 10)
Snowy Egret	13.5 (0.35, 8)	9.1 (0.39, 6)	12.9 (0.22, 6)
Little Blue Heron	13.3 (0.37, 7)	8.7 (0.73, 4)	11.5 (0.09, 4)

[1] Symbols as in Table 1.

VARIATION IN AIR SPEED

The variation of air speed is interesting because measurements in wind tunnels indicate that air speed may markedly influence the power expenditure in flight (Tucker, 1968, 1969). The most economical air speed depends on the goal of the flight and wind conditions. If the goal is to remain aloft the longest possible time, the most economical air speed is that where power expenditure is least. If the goal is to cover maximum distance over the ground, the most economical air speed is that where the ratio of power expenditure to ground speed (energy expended/distance traveled) is least. In the interests of energy conservation, one might expect that the air speeds of undisturbed birds in nature would be regulated to achieve one or the other of these goals.

The air speeds we measured are too variable to support the hypothesis that birds fly at closely regulated air speeds to conserve energy. For example, the speed range of Budgerigars (*Melopsittacus undulatus*) in level flight in a wind tunnel was 5.3 to 13 m/sec (12 to 30 mph) and over this range, power expenditure changed between 105 and 164 cal/(g hr) depending on speed (Tucker, 1968). The standard deviation of air speeds of Budgerigars in nature is unknown, but if it were 2.5 m/sec, a typical value for the present study, and air speeds in nature were normally distributed, they would completely cover the range observed in the wind tunnel and 10 per cent of them would exceed it. For the Laughing Gull in the wind tunnel, power expenditure ranged from 40 to 62 cal/(g hr) over a speed range from 8.6 to 12.5 m/sec (19 to 28 mph) (Tucker, 1969). Again the air speeds measured in nature completely cover this range. The speed where the gull in the wind tunnel covered distance most economically, 12.5 m/sec, agrees closely with the mean air speed in nature, 12.6 m/sec.

In the few other cases where the air speeds of birds have been measured frequently enough to indicate variability, air speed has a standard deviation of 2.7 m/sec (6 mph) or less. Michener and Walcott (1967) used an airplane and radio tracking to follow pigeons from distances of several kilometers. Individual birds flew at speeds that were "constant" within the accuracy for which wind velocity was known. The air speed values of Spiers (1945) for the Oldsquaw (*Clangula hyemalis*) have a standard deviation of 2.5 m/sec, and some of this variability may be due to the "quite considerable variation" in wind velocity. Lokemoen's (1967) values for ground speeds of Wood Ducks (*Aix sponsa*) flying in "negligible" wind have a standard deviation of 2.4 m/sec. Schnell's (1965) numerous radar records of ground speed for various birds flying in winds with speeds less than 3.6 m/sec (8 mph) have standard deviations between 1.2 and 2.7 m/sec.

Although the large variation of air speeds in nature does not support the hypothesis of a closely regulated air speed, neither does it deny it. Some of the variation in the air speeds we calculated may be due to changes in wind velocity in time and space that we could not measure and correct for, and to changes in flight direction (see below). Further testing of the hypothesis will depend on accurate measurements of air speed when the wind velocity is constant, preferably zero.

WIND DIRECTION

The birds we measured flying in headwinds, tailwinds, and crosswinds seemed to fly at different air speeds depending on wind direction, with the highest air speeds in headwinds and the lowest in tailwinds (Table 3). This phenomenon is worth comment because it could increase a bird's flight range in windy conditions (Pennycuick, 1969), and it has been described in two other studies. Bellrose (1967), using radar, found that the air speeds of birds migrating at night with tailwinds decreased as the speed of the tailwinds increased. Schnell (1965), also using radar, found that the air speeds of birds were highest in headwinds and lowest in tailwinds.

Although the evidence is suggestive that birds fly with higher air speeds in headwinds than in tailwinds, an alternate explanation is that the phenomenon is an artifact resulting from an overestimate of wind speed. Usually a bird's flight velocity is measured relative to the ground, and air speed is obtained after vector addition of ground and wind velocities. Thus if wind speed is overestimated, a bird flying at constant air speed would appear to have the highest air speed when flying into the wind, and the lowest air speed when flying with a tailwind. Three of our four species and all of Schnell's species that flew in the three wind directions have relations between air speeds in head-, tail-, and crosswinds that could be explained if air speed actually were constant but wind speed were overestimated. The observations of Bellrose also would be explained if wind speed were overestimated.

There is, in fact evidence that both Bellrose (1967) and Schnell (1965) have overestimated wind speed. Bellrose, for example, gives the following regression equation that describes the ground speeds of birds in knots (Y) at different tailwind speeds in knots (X):

$$Y = 36.3 + 0.32X. \qquad (1)$$

Since for a tailwind,

$$\text{Air speed} = Y - X, \qquad (2)$$

the above equations yield

$$\text{Air speed} = 36.3 - 0.68X. \qquad (3)$$

At X values above 20 knots, most of the air speeds described by equation (3) are for waterfowl (Bellrose, 1967). However waterfowl probably cannot fly for long at air speeds less than 10 m/sec (22 mph, 20 knots) (Pennycuick, 1969), and equation (3) indicates they would have air speeds lower than this in tailwinds above 24 knots (12 m/sec, 28 mph). Many of Bellrose's records were made in tailwinds above 30 knots (air speeds of 8.2 m/sec, 18 mph or 16 knots) and some tailwinds were as high as 60 knots (air speed of –2.3 m/sec, –5.2 mph, or –4.5 knots). The negative sign indicates that air flows from the tail to the head of the bird, an impossible situation in flight. Thus, the magnitudes of the tailwinds must have been overestimated if the values for ground speed are correct.

Schnell (1965) also has apparently overestimated wind speed in at least one case. His data for Cliff Swallows (*Petrochelidon pyrrhonota*) flying with a tailwind indicate that the birds had a mean air speed of –0.027 m/sec (–0.60 mph).

There remains the possibility that a bird might increase its flight range in windy conditions by flying faster into a headwind than through still air or with a tailwind. An obvious example of this phenomenon is a bird flying into a headwind and making no headway over the ground, so that its flight range is zero. If the bird flew faster, it would make headway and its flight range would increase.

Data for the Budgerigar and the Laughing Gull in the wind tunnel allow us to calculate how much each bird should change its air speed to maximize its flight range as wind speed changes. The air speed for maximum range in the Budgerigar changes relatively little with wind speed (Figure 2), and not at all in the Laughing Gull. Even if the Budgerigar makes the small adjustment in its speed to maximize its range as wind speed increases, the gain in range is small. The quantitative relations that lead to these conclusions are described below.

To maximize range, a bird should fly level at the speed where the least

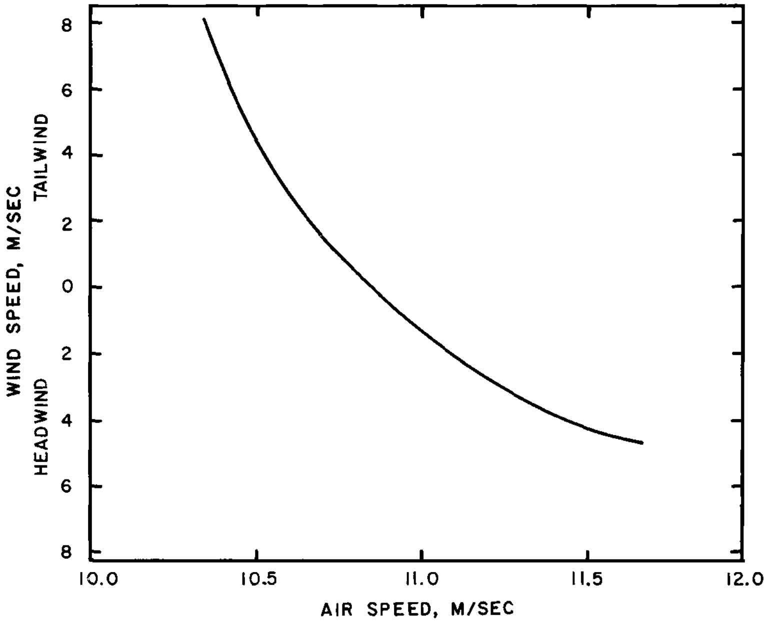

Figure 2. Air speeds at which a Budgerigar flying in various head- and tailwinds covers the maximum distance over the ground for a given energy expenditure.

energy is used to cover a given distance over the ground. Since the power required for level flight is a function of air speed (V), the energy (E) expended per unit distance traveled over the ground is

$$E = f(V)/(V + W) \qquad (4)$$

where f(V) is the power requirement for level flight; W is the wind speed and (V + W) is ground speed. W is positive for a tailwind and negative for a headwind.

If a minimum value for equation (4) exists, it may be found by differentiating with respect to V and setting the derivative equal to O. Under this condition, and with $f'(V) = df(V)/dV$,

$$W = [f(V) - Vf'(V)]/f'(V). \qquad (5)$$

The mean power expenditure of the Budgerigar in level flight is given by

$$f(V) = 0.074\ (V - 35)^2 + 22 \qquad (6)$$

where f(V) is cal/(g hr) and V is km/hr. This equation is calculated from Tucker (1968) and is accurate to better than 1 per cent at speeds between 35 and 48 km/hr (9.7 and 13 m/sec, 22 and 30 mph). Using equations (5) and (6), the air speed for maximum range increases only about 1.0 m/sec (2.2 mph) for an increase of 7 m/sec (16 mph) in wind speed from still air (Figure 2). Furthermore the bird cannot increase its range much by adjusting its air speed. For example the equations show that a Budgerigar flying in a headwind of 4.0 m/sec (9.0 mph) at the most economical air speed (11.5 m/sec or 25.8 mph) for that wind increases its range only 1.7 per cent above that attained by a Budgerigar flying in the same wind, but at the most economical air speed for still air (10.8 m/sec or 24.2 mph).

For the Laughing Gull, f(V) approximates a linear function (Tucker, 1969 and MS). This function has a positive intercept, so that in any head- or tailwind, the bird achieves its maximum range by flying as rapidly as possible.

If birds do fly at different air speeds depending on wind direction, they must have either some means of measuring their ground speed, or some means of getting information on wind direction from changes in wind velocity (turbulence). This is so because a bird cannot distinguish from the motion of the air relative to its body whether it is flying through still air or air moving at constant velocity relative to the earth. Birds flying relatively low and fast in daylight presumably can estimate ground speed visually, but it is more difficult to imagine how they could estimate ground speed with sufficient accuracy when migrating at night at an altitude of a kilometer and perhaps flying through or above clouds. Under these circumstances, changes in wind velocity may provide information about mean wind direction that enables birds to adjust their air speeds appropriately (Bellrose, 1967; Griffin, 1969).

ACKNOWLEDGMENTS

This study was supported by National Sciences Foundation Grant GB 6160X, Duke Endowment Grant 84 0926, and ONR Contract 1181. Mrs. Marsha Poirier provided technical assistance.

SUMMARY

A system of double theodolites measured velocity vectors for helium balloons and a variety of bird species flying in nature. The calculated air velocities of the birds were highly variable, although birds flying in a wind tunnel can minimize their rate of energy expenditure by flying at a particular velocity.

Birds appeared to have higher air speeds when flying in headwinds than in tailwinds. This phenomenon may be an artifact from errors in estimating wind velocity, but such behavior could maximize the range of a bird flying in windy conditions. The latter possibility is discussed in quantitative terms.

LITERATURE CITED

BAKER, E. C. S. 1922. Velocity of flight among birds. Brit. Birds, 16: 31.

BELLROSE, F. 1967. Radar in orientation research. Proc. 14th Intern. Ornithol. Congr.: 281–309.

BROUN, M., AND B. V. GOODWIN. 1943. Flight speeds of hawks and crows. Auk, 60: 487–492.

COOKE, M. T. 1937. Flight speed of birds. U. S. Dept. Agr., Circ. No. 428.

COTTAM, C., C. S. WILLIAMS, AND C. A. SOOTER. 1942. Flight and running speeds of birds. Wilson Bull., 54: 121–131.

GIBLETT, M. A. 1932. The structure of wind over level country. Meteorological Office, Geophysical Mem. No. 54, 6: 1–119.

GRIFFIN, D. R. 1969. The physiology and geophysics of bird navigation. Quart. Rev. Biol., 44: 255–276.

LANYON, W. E. 1962. A speed trap for birds. Nat. Hist., 71: 38–43.

LOKEMOEN, J. T. 1967. Flight speed of the Wood Duck (*Aix sponsa*). Wilson Bull., 79: 238–239.

MCCABE, T. T. 1942. Types of shorebird flight. Auk, 59: 110–111.

MEINERTZHAGEN, R. 1955. The speed and altitude of bird flight. Ibis, 97: 81–117.

MICHENER, M. C., AND C. WALCOTT. 1967. Homing of single pigeons—analysis of tracks. J. Exp. Biol., 47: 99–131.

PEARSON, O. P. 1961. Flight speeds of some small birds. Condor, 63: 506–507.

PENNYCUICK, C. J. 1969. The mechanics of bird migration. Ibis, 111: 525–555.

SCHNELL, G. D. 1965. Recording the flight-speed of birds by Doppler radar. Living Bird, 4: 79–87.

SPIERS, J. M. 1945. Flight speed of the Old-squaw. Auk, 62: 135–136.

THOMPSON, M. C. 1961. The flight speed of a Red-breasted Merganser. Condor, 63: 265.

TUCKER, V. A. 1968. Respiratory exchange and evaporative water loss in the flying Budgerigar. J. Exp. Biol., 48: 67–87.

TUCKER, V. A. 1969. The energetics of bird flight. Sci. Amer., 220: 70–78.

Department of Zoology, Duke University, Durham, North Carolina 27706, and *I. Zoologisches Institut der Universität, 3400 Göttingen, Berlinerstrasse 28, West Germany.* Accepted 26 January 1970.