

area may have re-nested elsewhere. Four cases of re-nesting where clutch-sizes were known for both initial and subsequent nests were observed. In all cases, the females involved were ASY and laid initial clutches of 4 eggs. Only 1 female laid 4 eggs in its second clutch; the other 3 females each laid only 3 eggs in their second clutches.

Acknowledgments.—I thank the C. K. Blandin Foundation and Wild Rice Growers' Association, Inc. for financial support; K. C. Carr and R. S. Wetzel (USFWS) for field support; H. Jacobson for permission to study the rice paddies; and M. W. Weller (University of Minnesota) for reviewing the manuscript. This paper is No. 10401, Scientific Journal Series, University of Minnesota Agricultural Experiment Station, St. Paul, Project 17-92.—DANIEL W. MOULTON, *Dept. Entomology, Fisheries and Wildlife, Univ. of Minnesota, St. Paul, Minnesota 55108.* (Present address: 70 Edgewood Dr., Central Valley, New York 10917.)
Accepted 1 Nov. 1979.

Wilson Bull., 93(1), 1981, pp. 121–124

Migration speeds of three waterfowl species.—To better understand the physical nature of bird migration and its energy requirements, it is important to evaluate the speed at which various species fly, and how speed may be affected by environmental factors. This paper reports on ground and air speed of migrating flocks of Canada Geese (*Branta canadensis interior*), Lesser Snow Geese (*Anser c. caerulescens*) and Mallards (*Anas platyrhynchos*).

In 1966, we began recording ground speeds of migrating waterfowl in central Illinois. By late 1978, we had obtained 160 records, all but 3 from a car driven for 1.5–24 km parallel to the birds' flight. The 3 additional records were obtained from mapping the course and time interval of migrating birds observed from a light aircraft. Migrating flocks of Canada Geese composed 79% of the records, Lesser Snow Geese 16% and Mallards 5% (Table 1).

At the time the waterfowl were observed, the wind direction and velocity were estimated. Direction data were more reliable than velocity estimates, which were based on radio reports and local clues (flag, foliage, smoke and the like). Most flocks were between 100 and 365 m above the ground. At those altitudes, wind direction was approximately the same as at ground level, but average wind velocity was probably higher. The wind force striking the migrating flocks was vectored on the basis of cosine of the angle of wind to migration track \times wind velocity.

Table 1 shows the ground speed of the migrants, the vectored air velocity assisting or impeding their passage, the calculated air speed that resulted from the deletion of the wind force and the statistical significance of the results. Data for the Canada Goose were separated into fall and spring periods to determine whether the stronger winds in the spring or the proximity of the wintering grounds were factors affecting the air speed of these geese.

A comparison of ground speed to the vectored wind speed shows that migrating Canada Geese adjusted their flight speed within certain constraints to compensate for wind velocity. Although the ground speeds of Canada and Snow geese flying into the wind were reduced, their effort (as measured by air speed) averaged 13.1 km/h; more when they flew against the wind than when they flew with it. The F value derived from an analysis of variance demonstrated a highly significant relationship between wind speed and the air speed of Canada Geese ($F = 18.5$, $P < 0.01$ for fall and 20.7 , $P < 0.01$ for spring), but no statistically significant difference in the Snow Goose ($F = 3.6$, NS). (The small sample measured in the opposed-wind category appears responsible.)

TABLE 1
THE EFFECT OF VECTORED WIND VELOCITY ON THE GROUND SPEED OF MIGRATING
FLOCKS OF WATERFOWL IN CENTRAL ILLINOIS, 1966-1978

Species	Season	No. of flocks	Ground speed (km/h)		Wind speed (km/h)		Corr. coeff.	P	Calcu- lated air speed (km/h)
			\bar{x}	\pm SD	\bar{x}	\pm SD			
Canada Goose	fall	48	72.7	\pm 6.4	+9.3	\pm 7.6	0.45	< 0.01	63.4
	fall	26	64.7	\pm 9.2	-12.2	\pm 9.8	-0.69	< 0.01	76.9
	spring	30	70.3	\pm 10.0	+13.0	\pm 10.5	0.22	< 0.10	57.3
	spring	22	60.7	\pm 6.0	-12.2	\pm 7.6	-0.39	< 0.10	72.9
Lesser Snow Goose	fall	21	83.3	\pm 5.1	+12.7	\pm 6.6	0.17	< 0.10	70.6
	fall	4	67.3	\pm 24.0	-13.4	\pm 8.8	-0.77	< 0.10	80.7
Mallard	fall	9	71.8	\pm 11.1	-18.8	\pm 12.2	-0.78	< 0.01	90.6

Within each wind force category (Table 1), linear regression demonstrated change in ground speed with wind speed. As the tail-wind force increased, migrants failed to correspondingly increase their ground speed. The correlation coefficient showed the best linear fit for the Canada Goose fall data. Spring wind data were more variable than fall data, perhaps as a result of a greater frequency of strong gusts at that season. Fig. 1 shows the effect of vectored wind velocity on the ground speed of migrating Canada Geese during the fall and the ground speed that might be expected without adjustment by the geese for wind force. The difference between the actual and projected ground speeds suggests that as favorable winds increase, the birds decrease their air speed and that as head winds increase, they fly faster. Several different plot tests showed that the relationship was linear rather than curvilinear.

The air speed of individual flocks of Canada Geese varied between 25 and 88 km/h. The instance of the highest speed recorded is especially interesting. At 07:15, 10 March 1977, Glen Sanderson and Bellrose were driving north on I-57 at Dix, Jefferson Co., Illinois, when they noticed 500 Canada Geese in 2 flocks migrating due north at an estimated altitude of 300 m. The geese had a ground speed of 96 km/h which they steadily maintained for the next 24 km. Local weather on the car radio indicated a south wind at 8 km/h. These geese had apparently just departed nearby Rend Lake, Jefferson Co., on a flight of about 185 km to a traditional spring concentration point on the Illinois River near Bureau, Bureau Co.

Because of this high air speed at the apparent onset of a migratory flight, we thought that spring air speeds might be higher than those in the fall because of energy expended on the longer fall flights. Central Illinois is closer to the winter grounds in southern Illinois than to James Bay or even Horicon Marsh, Wisconsin, points from which fall flights through Illinois emanate. However, air speeds of migrants were 4.2 km/h lower in the spring than in the fall ($F = 4.4$, $P < 0.05$). Apparently distance of flight does not appear to be a factor affecting flight effort.

With a following wind in the fall, the air speed of Snow Geese was 7.2 km/h greater ($P < 0.01$) than that of Canada Geese. The difference was significant ($F = 12.0$, $P < 0.01$). Flying against the wind in the fall, Mallard air speed also averaged 13.7 km/h faster than Canada Geese ($F = 21.4$, $P < 0.01$).

There is conflicting evidence regarding the effect of wind speed on the air speed of migrating birds. Blokpoel (Can. Wildl. Serv. Rept. Ser. 28:1-30, 1974) compared a small num-

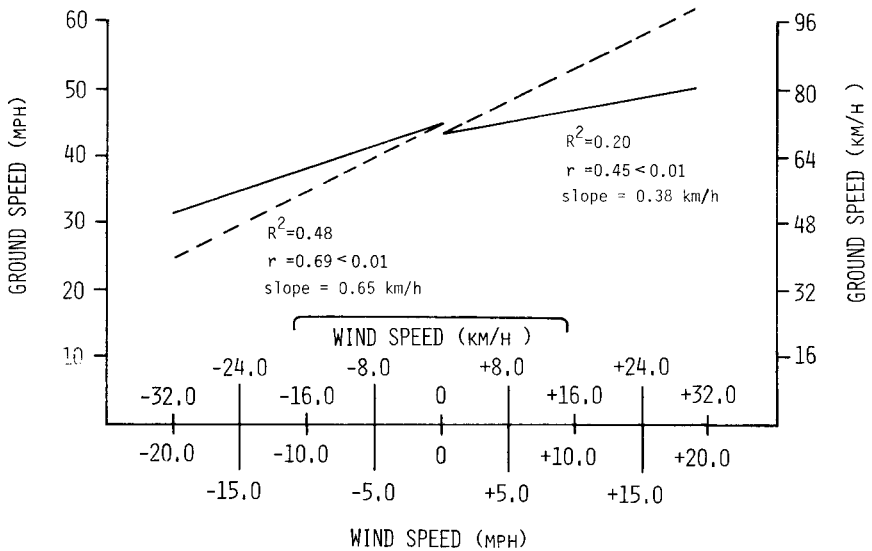


FIG. 1. Linear regression of the response of Canada Geese in ground speed to favorable wind speed and adverse wind speed. Dashed line indicates projected ground speed with no change in air speed.

ber of air speeds with wind speed records for migrating Lesser Snow Geese and concluded that wind speed resulted in little, if any, change in the air speed. Although Tucker and Schmidt-Koenig (Auk 88:97-107, 1971) found that air speeds of local birds varied with the component of the wind (head, tail or cross), they minimized the importance of energy conservation resulting from a bird altering its air speed, stating: "The air speeds we measured are too variable to support the hypothesis that birds fly at closely regulated air speeds to conserve energy."

On the other hand, Schnell (Living Bird 4:79-87, 1965) measured the local flight speeds of birds near the ground by Doppler radar and found that wind velocity affected the air speed of most birds. Bellrose (pp. 281-309 in Proc. XIV Int. Ornithol. Congr., 1967) noted that the speed of bird migrants on radar was not proportional to increases in wind speed, and suggested that migrants adjust their energy output in relation to the degree of wind assistance or resistance. Bruderer and Steidinger (pp. 223-258 in Animal Orientation and Navigation, S. R. Galler et al., eds., SP-262, U.S. Gov't. Print Off., Washington, D.C., 1972) used radar to ascertain that ground speeds of Chaffinches (*Fringilla coelebs*) in migration did not parallel increases in wind velocity; their decrease in air speed equalled about one-third the increase in wind force. In a further study of the flight speeds of 12 species of gulls (*Larus* sp.), terns (*Sterna* sp.) and skimmers (*Rynchops* sp.) near their nesting colonies, Schnell and Hellack (Am. Nat. 113:53-66, 1979) obtained additional evidence that bird air speeds usually varied inversely to wind speeds. Additional work by Tucker (pp. 298-333 in Avian Energetics, R. A. Paynter, Jr., ed., Publ. Nutt. Ornithol. Club No. 15, 1974) apparently led him to modify his views on the energy expended in flight: "At both sea level and altitudes of 6000 m, it is beneficial from an energetic point of view to fly faster into a head wind, and slower with a tail wind than is the case in still air."

Varying results obtained when comparing air speed of birds with wind speed may be a function of the wide range of air speeds that birds can use without the undue loss of energy. Schnell and Hellack (1979) concluded that “. . . air speeds can be increased or decreased considerably with only a relatively small increase in metabolic rate or cost of transport.” As shown by Greenewalt (Trans. Am. Philos. Soc. 65:1-67, 1975) cost of transport curves are relatively flat near their minima.—FRANK C. BELLROSE AND ROBERT C. CROMPTON, *Illinois Natural History Survey, Havana, Illinois 62644. Accepted 19 Dec. 1979.*