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Received 8 March 1988, accepted 6 January 1989.

Flight Range Estimates for Shorebirds

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Many models have been proposed to estimate the flight range of migratory birds. They derive either from aerodynamic theory (Pennycuik 1975, Greenewalt 1975), or from a combination of the fat loads of migratory birds and their associated costs of flight (McNeil and Caideux 1972). Aerodynamic models have not gained popularity among ornithologists because they require the input of variables not easy to measure. The other models utilize the cost of flight (i.e. Raveling and Lefebvre's [1967] or variations of the same) and require the input of flight speed, fat load, and body mass.

McNeil and Caideux (1972) used Raveling and Lefebvre's (1967) allometric equation to predict the cost of flight for shorebirds of a given body mass at takeoff. Summers and Waltner (1978) improved this model, and compensated for the effect of the decreased mass as the fat is consumed during flight. Finally Davidson (1984) modified the equation further. In addition to the mass decrease effect, he used the cost of flight for a nonpasserine bird estimated by Kendeigh et al. (1977).

Both the Raveling and Lefebvre (1967) and Ken-

deigh et al. (1977) equations predict that the cost of flight is a simple function of body mass. They assumed no benefits from environmental conditions such as favorable winds. Castro and Myers (1988) developed new equations empirically that allow the calculation of the cost of flight from body mass and morphometric variables related to aerodynamic characteristics, specifically wing length. When compared with flight costs actually measured using doubly labeled water, the estimates of this equation are remarkably more accurate than predictions using any other equation.

We calculated the costs of flight using the equations of Raveling and Lefebvre (1967), Kendeigh et al. (1977), and Castro and Myers (1988), for six species of shorebirds that vary in size from 25 to 428 g (Table 1). When expressed as multiples of basal metabolic rates (BMR), the first two equations predict very similar costs of flight for all the species, while the third equation predicts increasing costs of flight with increasing body mass.

The reason for this fundamental divergence is that the slope of the first two equations is similar to the slope that relates BMR to body mass, and implies that the cost of flight is a simple multiple of BMR. The slope of the third equation is a function of both body mass and aerodynamics. Therefore, the calculated values for the cost of flight are not a simple multiple of

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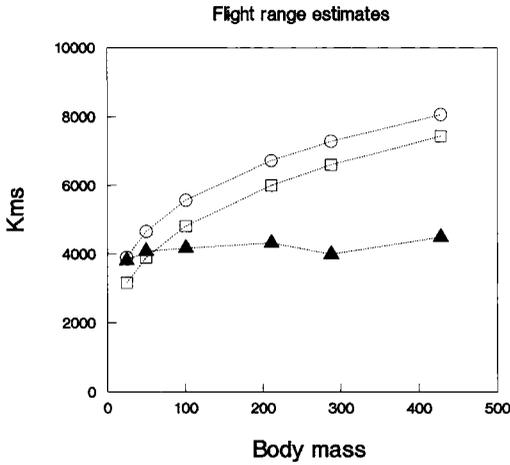


Fig. 1. Flight range estimates in km, using the equations of Summers and Waltner 1978 (O), Davidson 1984 (□), and this study (▲), for the 6 species in Table 1. We assumed that individuals depart with a fattening level of 40% (fat/total body mass), and that flight speed is 75 km/h.

BMR, but vary in an indefinite way (depending on the aerodynamics of the bird), therefore diverging from the classic 0.7 exponent of metabolic costs vs. body mass. This is not surprising, because two birds of the same mass can have remarkably different costs of flight depending upon their aerodynamic design (Castro and Myers 1988).

Furthermore, new information shows that shore-

birds in general have high BMRs (Kersten and Piersma 1987, Castro 1987). As a result, flight costs calculated using equations 1 and 2 are significantly lower than the classical "12 times BMR." This was pointed out by Summers et al. (1987), who doubted the validity of any flight range equations until real estimates of shorebird flight costs become available.

We developed a new model to estimate shorebirds' flight ranges based on the analysis by Castro and Myers (1988) of flight cost and, at the same time, allowed for the decrease in body mass during the migratory flight. This new equation was calculated following the integration procedure of Summers and Waltner (1978), and starting with the general equation,

$$R = S \cdot 39.5 \cdot F \cdot CF^{-1},$$

where R = flight range (km), S = flight speed (km/h), F = fat (g), CF = cost of flight (kJ/h), and 39.5 is a conversion factor (kJ/g of fat).

Therefore, the distance δR covered for each change in body mass δM (assuming that every change in body mass is due to fat utilization) is

$$\delta R = S \cdot 39.5 \cdot \delta M \cdot CF^{-1}.$$

Replace the cost of flight by the equation of Castro and Myers (1988):

$$\delta R = S \cdot 39.5 \cdot \delta M \cdot (3.167 \cdot M^{1.464} \cdot L^{-1.614})^{-1},$$

where L = wing length (cm) and M = body mass (g). Consequently, the distance covered while body mass decreases from M_2 to M_1 is

TABLE 1. Cost of flight for 6 shorebird species using 3 equations. Cost of flight as a multiple of BMR is in parentheses.

	Body mass ^a (g)	Wing length ^b (cm)	BMR ^c (kJ/h)	Eq. 1 ^d (kJ/h)	Eq. 2 ^e (kJ/h)	Eq. 3 ^f (kJ/h)
<i>Calidris pusilla</i>	25	9.8	1.23	12.16 (9.8)	9.85 (8.0)	8.85 (7.2)
<i>Calidris alba</i>	50	12.5	2.05	19.62 (9.5)	16.45 (8.0)	16.50 (8.0)
<i>Arenaria interpres</i>	101	15.5	3.42	31.88 (9.3)	27.68 (8.1)	32.64 (9.5)
<i>Pluvialis squatarola</i>	211	19.6	5.85	53.00 (9.0)	47.75 (8.1)	65.71 (11.2)
<i>Cataprophorus semipalmatus</i>	288	20.4	7.35	65.69 (8.9)	60.11 (8.2)	97.15 (13.2)
<i>Numenius phaeopus</i>	428	24.6	9.81	86.35 (8.8)	80.59 (8.2)	128.26 (13.1)

^a From Myers unpubl.

^b Average from Hayman et al. (1986).

^c Basal Metabolic Rate, from Kersten and Piersma (1987).

^d From Raveling and Lefebvre (1967).

^e From Kendeigh et al. (1977), nonpasserines.

^f From Castro and Myers (1988): Cost of flight = $3.167 \cdot M^{1.464} \cdot L^{-1.614}$, where M = body mass (g) and L = wing length (cm).

$$R = \int (S \cdot 39.5 \cdot M^{-1.464} \cdot L^{1.614}) \cdot 3.167 \delta M^{-1}$$

$$R = 26.88 \cdot S \cdot L^{1.614} \cdot (M_1^{-0.464} - M_2^{-0.464}),$$

where R = flight range (km), M_1 = body mass at the end of the flight (g), M_2 = body mass at the start (g), S = flight speed (km/h), and L = wing length (cm).

The flight ranges for the species of Table 1, for flight speeds of 75 km/h and a fattening level of 40% (fat/total mass), are predicted in Fig. 1. The first two models predict a rapidly increasing flight range with increasing body mass. In contrast, our model predicts similar flight ranges for big and small species. This result is important, because it suggests that birds with similar aerodynamic designs (shorebirds in this case) have similar flight range values. Although we concur with Summers et al. (1987) on the need for direct measurements in migratory flight, we believe that this new equation provides a more realistic approximation to the flight range capabilities of shorebird species, because it uses both body mass and aerodynamic characteristics, and at the same time allows for the decrease in body mass during the migratory flight.

T. Piersma, R. Summers, D. Raveling, and A. H. Brush provided many important comments in the original manuscript.

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Received 2 August 1988, accepted 22 January 1989.

Impact of Brown-headed Cowbird Parasitism on the Reproductive Success of the Solitary Vireo

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The Solitary Vireo (*Vireo solitarius*) is sympatric with the Brown-headed Cowbird (*Molothrus ater*) in eastern and western North America (A.O.U. 1983). Although the Solitary Vireo has been mentioned as an occasional cowbird host, especially in the western United States (Friedmann 1971, Friedmann et al. 1977, Friedmann and Kiff 1985), little information exists on the timing, extent, or effects of cowbird parasitism. We describe the reproductive interactions of the Brown-headed Cowbird and the Solitary Vireo (*V. s. plumbeus*) in Colorado.

Vireo nest data were collected during the summers

of 1984-1986 in the foothills of the Rocky Mountains west of Boulder, Colorado. Study sites ranged from 1,800 to 2,120 m in elevation. These areas were dominated by ponderosa pines (*Pinus ponderosa*) and scattered Douglas fir (*Pseudotsuga menziesii*). The vegetation had a parklike appearance, with an open canopy and widely spaced ponderosa pines. The herb-shrub stratum was sparse and consisted of seedlings and saplings of the dominant tree species, Rocky Mountain Maple (*Acer glabrum*), willows (*Salix* spp.), chokecherry (*Prunus virginiana*), kinnikinnick (*Arctostaphylos uva-ursi*), squawbush (*Rhus trilobata*), snowberry (*Sym-*