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Received 30 August 1993, accepted 20 November 1993.

The Auk 112(1):260-262, 1995

Water and Energy Limitations on Flight Range

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Carmi et al. (1992) proposed a computer model that furthers our knowledge of whether energy or water are the greater physiological limitation to bird flight range. With the trans-Saharan migrating Willow Warbler (*Phylloscopus trochilus*) as an example, the model is a major theoretical effort to identify several important parameters on which migratory research should be focused in the future. However, there is a shortcoming in the model, as it calculates the flying bird's energy and water budget largely independent of each other. Only the calculated energy-consumption rate in the energy budget part of the model is passed to the water-budget component for the calculation of respiratory water loss and metabolic water production. However, the usual negative water balance, as pointed out by Carmi et al. (1992), will result in a decrease of body mass that should be accompanied by changes in optimal flight speed and costs of flight. Thus, water and energy budgets influence each other mutually.

I adjusted the model by Carmi et al. to account for this continuous change in body mass due to water loss (in their energy-budget part, Carmi et al. used Pennycuick's [1989] flight-range model, which already accounts for mass loss as a result of use of energy reserves underway). In the alternative "extended" model, where the energy and water budgets of the flying bird are closely linked, the model's parameter values change continuously during flight performance. To approximate these continuous changes, all parameters were evaluated and actualized at 15-min flight intervals. In this commentary, I will discuss some of the major discrepancies that occur between the original model of Carmi et al. (1992) and the extended model outlined above.

For this comparison, in concordance with Carmi et al.'s paper, I simulated the flight of a small Palaearctic passerine, the Willow Warbler (with a wingspan of 0.17 m and an initial body mass of 10 g, including 5 g water [of which a 30% loss is tolerated] and 3 g fat), during its annual migration over the Sahara desert. When not stated otherwise, a flight altitude of 2,000 m, an air temperature of 14 °C, and an oxygen-extraction coefficient of 0.039 are assumed, all in accord with the parameter settings used by Carmi et al. (1992).

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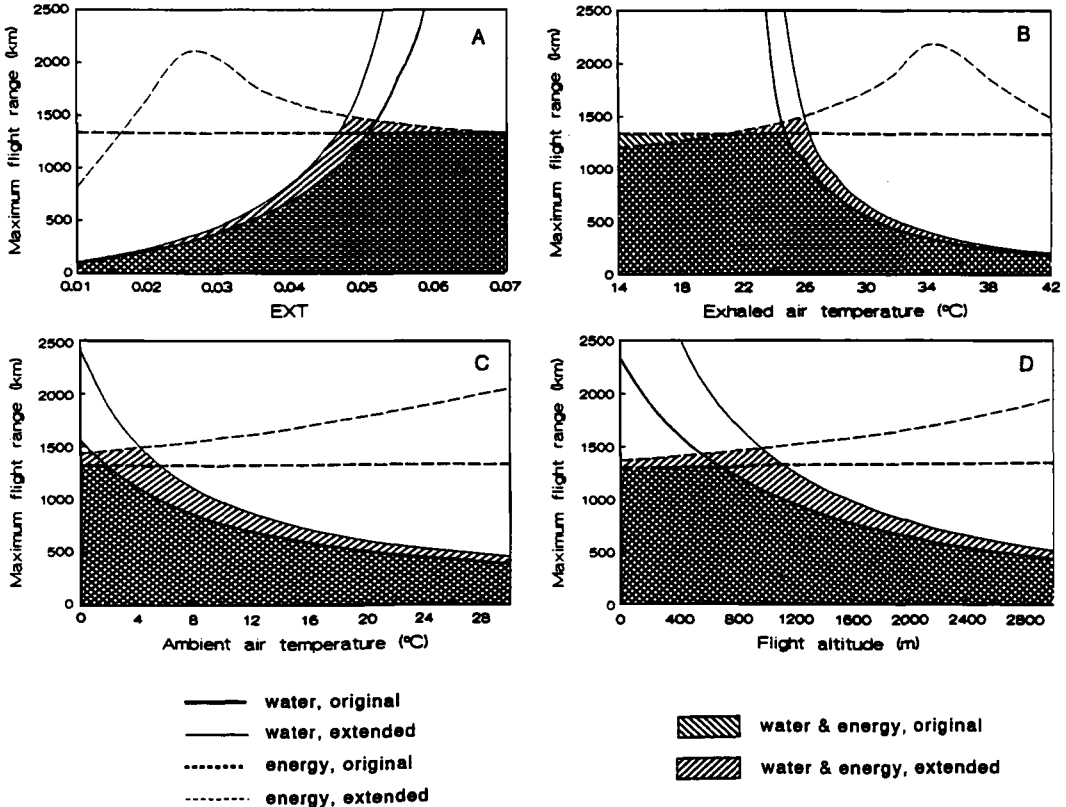


Fig. 1. Relations of flight range with isolated effect of (A) oxygen extraction, (B) exhaled air temperature, (C) ambient air temperature, and (D) flight altitude (impinging on oxygen partial pressure and air density) for a small passerine traversing Sahara desert. Solid lines designate limitation to flight duration imposed by a maximum allowable water loss and dashed lines designate energy limitation imposed by use of all stored body fat. Thick lines are predictions according to original model of Carmi et al. (1992) and thin lines are predictions of extended model, where the energy and water budgets of the flying bird are more interlooped. Hatched areas refer to possible flight range accounting for both water and energy limitation according to original and extended models.

Exhaled air temperature is calculated from ambient temperature according to Berger et al. (1971). For all other default parameter settings and a detailed description of the model, see Carmi et al. 1992.

The close concordance that exists in the original model between flight duration and flight range fades in the extended model because optimal flight speed critically depends on body mass (Pennycuik 1989), which changes less predictably in the extended compared to the original model. I abstain from comparing flight durations and will evaluate the differences between the original and extended model in terms of flight-range differences only. Each model yields both a flight-range estimate on the basis of the tolerances in the water (water flight range) and in the energy budget (energy flight range). Since further flight is theoretically impossible beyond the lowest flight-range estimate of the two, the other and higher estimate loses its relevance. Thus, one should pay at-

tention mainly to the lowest of the two range estimates, which I call the "possible flight range" (corresponding with hatched areas in Fig. 1). I discuss the effect of four parameters shown by Carmi et al. (1992) to be of paramount interest on flight range.

For a range of oxygen-extraction coefficients, the water flight ranges are always larger when calculated with the extended compared to the original model (Fig. 1A). Due to rapid water loss at low oxygen-extraction values, the energy flight ranges also are low in the extended model. However, they rapidly increase with oxygen extraction, overshooting the energy flight range estimates of the original model reaching a peak at an oxygen extraction of 0.026, slowly decreasing afterwards. In the lower range of oxygen-extraction values, water reserves are limiting the flight range. Above an oxygen extraction of 0.047 in the extended and 0.052 in the original model, energy reserves limit the flight range. For the extended mod-

el the possible flight ranges always are larger, and an optimum (i.e. where energy flight range equals water flight range) is reached at a lower oxygen-extraction value than predicted by the original model.

Varying exhaled air temperature (Fig. 1B) reveals principally the same results as outlined above for the oxygen-extraction coefficient in Figure 1A. Only here the energy flight range of the extended model is lower at low exhaled air temperatures due to respiratory water intake resulting in an increase in body mass and, thus, flight costs. Clearly, a possible body-water surplus should be easy to compensate through urinary losses. Assuming a body-water surplus does not occur, flight ranges calculated with the extended model always are equal to or larger than those calculated with the original model. The optimal flight range in the extended model is reached at a higher exhaled air temperature than calculated with the original model. With varying ambient temperature (Fig. 1C) and flight altitude (Fig. 1D), flight ranges calculated with the extended model always are larger than those of the original model. In the extended model, the maximum flight range is reached at a higher ambient temperature and flight altitude.

The extended model predicts that, when the expected meteorological conditions aloft are favorable for water economy, water should possibly be lost before take off. However, the meteorological conditions under which water balance would be positive are seldom if ever encountered. For the ranges in ambient temperature and altitude in Figures 1C and 1D, where energy is the limiting source, a careful tuning in pre-flight water reserves would have resulted in a minor gain in possible flight range.

Although it is generally believed that energy, rather than water, is the major factor limiting bird flight (e.g. Biebach 1990), with a small trans-Saharan migrating passerine as an example, Carmi et al.'s model makes it plausible that the threat of dehydration places a great physiological constraint over an array of possible meteorological conditions.

Although the extended model does not change anything basically with respect to this conclusion, predictions of the extended model are more favorable for the Palearctic passerine crossing the Sahara des-

ert than foreseen by the original model. Not only are flight ranges always longer than originally calculated, the optimal flight ranges also are reached under more realistic physiological and climatological conditions.

Figures 1A and 1B show that, on the basis of the extended model, adaptations for prolonged flight aiming at an increase in oxygen extraction and a decrease of exhaled air temperature, need not be as pronounced as predicted by the original model. Carmi et al.'s model predicts optimal flight ranges at low ambient temperatures and low altitude. However, ambient temperature tends to decline with increased altitude, making the optimal choice of the migrant one between two opposing factors. In the extended model, however, both the optimal altitude and ambient temperature are higher, making the choice more achievable for a trans-Saharan migrant. Clearly, at this stage, one cannot advance much further the discussion of whether energy or water are the major limiting sources during trans-Saharan migration without accurately knowing flight altitudes of migratory birds and meteorological conditions aloft, including wind direction and speed. Indeed, such data incorporated in the slightly adapted model of Carmi et al. (1992) could greatly advance our knowledge of the factors limiting migration and the impact of possible physiological adaptations.

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Received 17 December 1992, accepted 1 July 1993.