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Recent experimental data on the energy costs of avian flight call for a revision of optimal migration theory.—Optimal migration theory is the established paradigm in the study of avian migration (Alerstam and Lindström 1990, Weber and Houston 1997, Hedenström 2008), and most recent studies of migration strategies and tactics are performed within this framework (e.g., Eichhorn et al. 2009, Henningson et al. 2009). The central assumption of this theory is that the flight-range equation is a diminishing return function of added fuel mass:

$$Y(f) = c \left(1 - \frac{1}{\sqrt{1+f}} \right) \quad (1)$$

where Y is the flight range, f is the relative fuel load, and the constant c includes factors related to the bird's aerodynamic quality, fuel composition, muscle work efficiency, and aerodynamic conditions (Alerstam and Lindström 1990, Hedenström 2008). Weber and Houston (1997) generalized Equation 1 and showed that different flight-cost estimates available to them could be summarized as

$$Y(f) = c[1 - (1+f)^{-\zeta}], \quad 0 < \zeta < 1 \quad (2)$$

The most important consequence of this assumption is that increases in fuel deposition represent a case of diminishing returns because the more fuel a migrant deposits, the smaller the increment in potential flight distance becomes because of the cost of transport of the extra load.

Another relationship of profound importance for optimal migration theory is the one between flight speed and the power of flight. This relationship is widely accepted as being described by the following formula:

$$P(v) = \alpha + \beta \times v^{-1} + \gamma v^3 \quad (3)$$

where P is flight power, v is flight speed, and α , β , and γ are physical parameters of the air and the bird (Pennycuik 1989; Hedenström 2002, 2008). This function is U-shaped (Fig. 1), which means that there is a single minimum power speed value, above and below which energy expenditure increases.

Both of these crucial relationships are based on mechanical flight theory (Pennycuik 1975, 1989; Lindhe Norberg 2004; Hedenström 2008). However, neither of them is fully supported by recent experimental data.

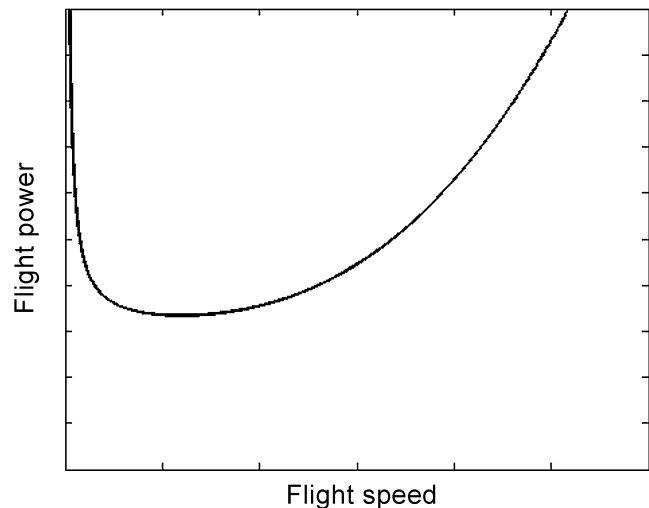


FIG. 1. Power required for a bird to fly by horizontal flapping flight in relation to its air speed, based on Equation 3.

Four recent studies measured energy costs of several hours of flight in wind tunnels in relation to intraspecific variation in body mass (Kvist et al. 2001; Engel et al. 2006; Schmidt-Wellenburg et al. 2007, 2008). Flight costs in Rosy Starlings (*Sturnus roseus*) were shown to increase with $m^{0.55}$ (95% confidence interval [CI] of the scaling exponent: 0.36–0.75; Engel et al. 2006). In another study of the same species, the scaling exponent was 0.57 (95% CI: 0.40–0.74) if the data for birds carrying harnesses and those not carrying were pooled for analysis, and 0.47 (95% CI: 0.18–0.76) if only the birds with harnesses (loaded and unloaded) were included (Schmidt-Wellenburg et al. 2008). In the Barn Swallow (*Hirundo rustica*), the scaling exponent was 0.58 (95% CI: 0.19–0.97; Schmidt-Wellenburg et al. 2007), and in the Red Knot (*Calidris canutus*) it was 0.35 (95% CI: 0.08–0.67; Kvist et al. 2001). All these values are clearly below 1; that is, flight costs increase much less steeply than assumed by the accepted aerodynamic theory (scaling exponent: 1.1–1.6; Norberg 1990, 1996; Pennycuik 1975; Rayner 1990). The flight-range equation can be obtained by integrating the flight-power equation (Weber and Houston 1997: equation 9):

$$\frac{dY}{dM} = \frac{v(M) \times E}{P(M)} \quad (4)$$

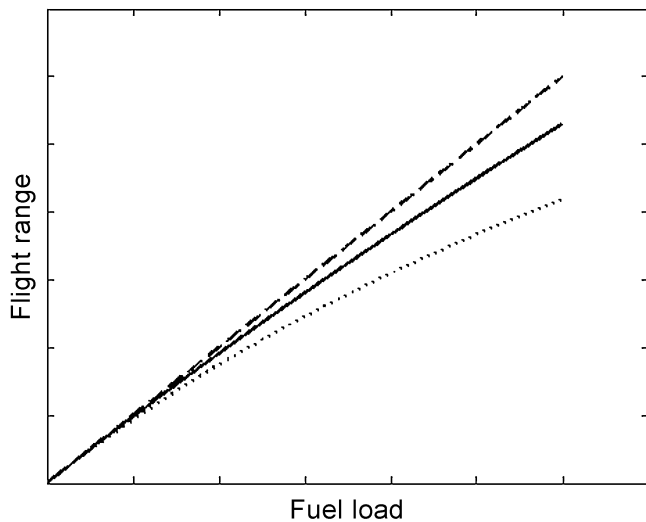


FIG. 2. Gain in flight range with increasing fuel load. The dotted line represents flight range proportional to $f^{-0.5}$ (function based on Equation 1), the solid line represents flight range proportional to $f^{0.5}$, and the dashed line represents flight range proportional to f (linear relationship).

where $v(M)$ is mass-dependent flight speed, E is energy density of fuel stores, and $P(M)$ is the flight-range equation. If we ignore the mass dependence of flight speed, this means that $Y(f)$ is proportional to $(1 + f)^\zeta$, where $\zeta > 0$ (cf. Equation 2). Clearly, the calculations of flight and stopover parameters are affected by these results, because this relationship deviates less from the linear function than Equation 1 (Fig. 2).

Most reviews have claimed that the U-shaped relationship between flight speed and flight power is well supported by the experimental data (Schmidt-Nielsen 1997, Blem 2000, Harrison and Roberts 2000). Only Ellington (1991) emphasized the scarcity of data to support this claim. Here, I update Ellington's (1991) review, including more recent measurements, and discuss implications for optimal migration theory. Until recently, the U-shaped relationship predicted by mechanical flight theory (Fig. 1) has been supported by a single study involving a single species, the Budgerigar (*Melopsittacus undulatus*; Tucker 1968), whereas other studies showed either a weak positive relationship, as in the Laughing Gull (*Leucophaeus atricilla*; Tucker 1972), Fish Crow (*Corvus ossifragus*; Bernstein et al. 1973), and European Starling (*Sturnus vulgaris*; Ward et al. 2004), or similar flight power across a wide range of flight speeds, as in European Starling (Torre-Bueno and Larochelle 1978), Barnacle Goose (*Branta leucopsis*), and Bar-headed Goose (*Anser indicus*; Ward et al. 2002). A recent wind-tunnel study showed independence of flight costs from flight speed in Rosy Starlings despite a 55% increase in flight speed (Engel et al. 2006). A clearly U-shaped relationship between flight power and speed was shown by *in vivo* measurements of muscle force in Cockatiels (*Nymphicus hollandicus*), whereas the relationship was weakly U-shaped in Ringed Turtle-Doves (*Streptopelia risoria*; Tobalske et al. 2003) and flat in Black-billed Magpies (*Pica pica*; Dial et al. 1997). Recently, a U-shaped relationship was reported for the Budgerigar and Cockatiel (Bundle et al. 2007). It

is noteworthy that both cases of the unequivocally U-shaped relationship involved species that do not migrate long distances. Berger (1985) found J-shaped relationships in the Sparkling Violetear (*Colibri coruscans*) and Green Violetear (*C. thalassinus*); their flight metabolism did not vary significantly between hovering speeds and up to $7 \text{ m}\cdot\text{s}^{-1}$ (which is a quite significant speed for a bird of this size). At even higher flight speeds, metabolic rate increased.

Thus, both main theoretical assumptions on which optimal migration theory is based are not supported by most empirical data. When fuel stores are low, the relationship between potential flight range and relative fuel stores deviates from the linear proportionality less than assumed by Equation 1 (Fig. 2). Under such conditions, flight cost is low, and it becomes higher and in better agreement with the predictions of the current aerodynamic flight theory with increasing fuel stores. This is supported by the data on escape flights of Blackcaps (*Sylvia atricapilla*; Kullberg et al. 1996) and Sedge Warblers (*Acrocephalus schoenobaenus*; Kullberg et al. 2000). The authors claimed that flight speed and acceleration decreased with increasing fuel load, but this effect was apparent only when fuel load exceeded 30% of lean body mass (Kullberg et al. 1996: fig. 3, Kullberg et al. 2000: fig. 1). Current calculations of optimal migration theory may approach reality for birds that cross large ecological barriers (e.g., the Sahara or the Gulf of Mexico) and carry large fat stores, but this is an interesting special case of avian long-distance migration. Most passerines that migrate over suitable habitats with continuous stopover possibility usually carry moderate fuel stores <30% of their lean body mass (Bairlein 1991, 1997).

U-shaped flight-power curves appear to be just a special case probably confined to some birds of low aerodynamic capacity, or at least to those whose annual cycle does not include long-distance migration. Most birds that spend a significant proportion of their time flying seem to be able to fly equally efficiently across a wide range of speeds. The data on parrots and hummingbirds emphasize that this ability is certainly not unlimited, but migrants seem to fly quite efficiently across the range of speeds they routinely employ. Aerodynamic calculations that predict mass exponents ranging between 1.1 and 1.6 (Pennycuik 1975, 1978; Rayner 1990; Norberg 1996) and a U-shaped flight-power curve are based on fixed-wing theory and are apparently not relevant for modeling avian flight (Dolnik 1995, Videler 2005). This means that the concepts of distinct minimum-power speed, maximum-range speed, and speed of time-minimizing migration (e.g., Hedenström 2008) also need to be reevaluated and probably revised.

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