Recent Experimental Data on the Energy Costs of Avian Flight Do Not Call for aRevision of Optimal Migration Theory

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Recent experimental data on the energy costs of avian flight do not call for a revision of optimal migration theory.—In a recent letter, Chernetsov (2010) questioned the validity of two fundamental relationships of animal flight mechanics and, as a consequence, argued that optimal migration theory is in need of revision. The first equation is the "flight-range equation" that describes the potential flight range as a function of fuel load, which is an important assumption when deriving, for example, the optimal fuel departure load and stopover duration (Alerstam and Lindström 1990, Hedenström and Alerstam 1997), overloading and bypassing of potential stopovers (Gudmundsson et al. 1991), and departure in relation to varying winds (Weber et al. 1998, Weber and Hedenström 2000). The flight range depends on two factors of the fuel load: (1) the added weight of the fuel, which increases the induced drag of lifting a heavier body against gravity; and (2) the added drag caused by the subcutaneous fat deposits due to increased projected frontal area (Alerstam and Hedenström 1998). Let the relative fuel load $f = m/m_0 - 1$, where m is body mass, including fuel, and m_0 is the lean body mass. If we assume that the body length is unaffected by added fuel and that the fat is stored uniformly around the body, the potential flight range as a function of relative fuel load f is

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

where the coefficient c includes several factors, such as fuel composition, energy conversion efficiency, bird morphology, and acceleration due to gravity and wind. This is the original flight-range equation used to derive predictions about stopover duration, overloading and bypassing, and responses in relation to winds (e.g., Alerstam and Lindström 1990, Gudmundsson et al. 1991, Weber et al. 1998). Subsequent studies of the pattern of fat deposition in a few passerine birds show that fat is not deposited uniformly around the body (Wirestam et al. 2008); rather, relatively more fat is deposited at the front and back ends of the body (although without making the bird longer). Thus, the shape of the bird changes during fuel deposition. However, the frontal area—and, hence, drag—still increases with added fuel load (Wirestam et al. 2008). If the frontal area is unaffected by added fuel, the flight-range equation takes the following form (Alerstam and Hedenström 1998):

$$Y(f) = \frac{c}{2}\ln(1+f) \tag{1B}$$

Therefore, the true flight range lies somewhere between Equations 1A and 1B. Qualitative predictions, however, are very similar regardless of which version of the flight-range equation is used, with the exception that overloading and bypassing are never optimal if Equation 1B is used. Even if the constant c affects the absolute potential flight distance, it conveniently cancels out from the derivations of optimal fuel loads and stopover durations under different conditions of search or settling costs and fuel deposition rates. What is important is the diminishing return utility of the flight-range equation, which is characteristic in both Equations 1A and 1B. Chernetsov (2010) pointed out that a few empirical studies show a less-than-expected (from aerodynamic theory) increase in flight cost in relation to within-individual variation in body mass (but see Kvist et al. [1998] for a case in which the increase is higher than expected). The reason for this discrepancy is not fully understood, but the increase in flight cost confirms the diminishing return utility of added fuel mass and, hence, that the fundamental flight-range equation is not compromised. Also, Chernetsov (2010) cited studies of escape flight performance (e.g., Kullberg et al. 1996, 2000) to support his claim that the validity of Equation 1 is not supported by empirical data. However, even if relatively small fuel loads had little effect on escape flight performance, such experiments are irrelevant to the relationship between fuel load and potential flight range, because they usually measure a sprint flight response in relation to a perceived predation risk.

The second fundamental relationship questioned by Chernetsov (2010) was the relationship between power required and air speed, $P(U)$, which is predicted to assume a U-shape (Pennycuick 2008). There is an immediate appeal to this function, often referred to as the "power curve," because it suggests ecologically significant flight speeds that a bird "should" select depending on ecological context (e.g., Hedenström and Alerstam 1995). For example, if birds are concerned with minimizing the energy cost per unit of time without paying attention to the distance moved, the minimum power speed (U_{mp}) is the best choice, whereas if energy cost per unit distance covered is important, the higher maximum range speed (U_{mr}) is the best option. Following a selective review of published studies, Chernetsov (2010) claimed that "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." However, a more complete review of published information gives a different picture (Engel et al. 2010).

The flight mechanical theory predicts a U-shaped relationship between mechanical power required to fly and air speed

(Pennycuick 2008), whereas the majority of studies concern measurement of flight metabolic rate. With a constant energy conversion efficiency, there should be a direct correspondence between mechanical power and flight metabolic rate ("chemical power"). Metabolic power has been measured in wind tunnels by three different methods (Engel et al. 2010): (1) using a respirometry mask attached to the bird (13 studies), (2) using a sealed wind tunnel as a respirometry chamber with unrestrained birds (1 study), and (3) using doubly labeled water (1 study). Out of these 15 studies of the chemical power curve, 5 showed a clear U-shaped curve and 6 showed an increase of power at high speeds. Four studies showed flat curves, which could be attributed to the fact that a limited speed range was investigated (in studies that resulted in a flat curve, average speed range = 6.4 m s^{-1}; in studies that resulted in U-shaped curves, average speed range = 9.1 m s^{-1}). In one of the studies that obtained a flat power-curve, a speed range of 10 m s^{-1} was investigated (Torre-Bueno and Larochelle 1978). A recent study, not included in Engel et al. (2010), added Allen's Hummingbird (*Selasphorus sasin*), a migrating species, to the group of U-shaped chemical power curves (Clark and Dudley 2010). For graphic illustration of different power curves, the reader is referred to Rayner (1999). In addition, wind-tunnel studies of four bat species likewise showed the existence of a U-shaped power curve (Hedenström et al. 2009). The few studies that have estimated mechanical power on the basis of measurements of muscle work showed U-shaped power curves, with two possible exceptions (Dial et al. 1997, Pennycuick et al. 2000). The possible exceptions showed an L-shaped curve (high values of estimated power at zero speed, followed by a decline in power to a minimum at 6 m s^{-1} and thereafter only a marginal increase in power between 6 and 14 m s^{-1} resulting in a perceived L-shaped relationship between power and speed; Dial et al. 1997), whereas one study showed an increase of power with increasing speed. Again, in the latter of these studies, the result could be attributed to a limited speed range being investigated (Pennycuick et al. 2000). The overall conclusion from this review of the literature is that the available data cannot be used to refute the existence of a U-shaped power–speed relationship in bird flight (Engel et al. 2010).

In addition to the direct measurements of the power curve itself, there is behavioral support for the existence of a U-shaped power curve. A U-shaped power curve predicts characteristic flight speeds, such as the minimum power speed (U_{mp}), associated with the minimum flight cost per unit of time, and the maximum range speed (U_{mr}) associated with the minimum cost per unit distance covered. It appears that Sky Larks (*Alauda arvensis*) are able to appropriately select flight speed in different ecological situations, such that a speed close to U_{mp} is selected in song display flight, whereas a much higher speed (U_{mr}?) is selected during migration (Hedenström and Alerstam 1996). Similar context-related flight speed selection has also been shown for a bat (Grodzinski et al. 2009).

Predictions about migration strategies are based on Equation 1, with additional assumptions about some immediate "currency" such as energy, time, or safety. For example, the "time minimization hypothesis" predicts a positive relationship between departure fuel load (f_{dep}) and realized fuel deposition rate (FDR) at stopovers (Alerstam and Lindström 1990, Hedenström and Alerstam 1997). Most field experiments in which these variables have been monitored in individually color-banded birds have found a positive relationship between f_{dep} and FDR (Hedenström 2008),

which suggests that time is an important factor in bird migration. However, the slope of this relationship can tell whether there are additional factors involved or whether birds update their future expectations about FDR along the migration route on the basis of current experience (Houston 1998). Chernetsov (2010) called for a revision of optimal migration theory, but I argue that his reasoning is based on selective reading of the literature and the use of irrelevant information (such as the takeoff flight experiments he cites as evidence against the validity of Equation 1). Migration theory has been augmented and revised over the past 20 years (Alerstam 2011) and, as with most scientific theories, it cannot explain all aspects about bird migration. However, it remains a very useful tool for generating predictions about migration strategies and behaviors that can be tested by observations or experiments. Discrepancies between a prediction and an empirical observation, either qualitative or quantitative, have to be looked for among the decision and currency assumptions or the choice principle used (Stephens and Krebs 1986). Many predictions have withstood the test by empirical data, whereas others remain to be tested critically. I am convinced that optimal migration theory will continue to play an important and productive role in bird migration studies and that it will be further developed and refined.

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Optimal migration theory: Response to Hedenström (2012).—In my 2010 paper (Chernetsov 2010), I questioned whether sufficient data existed to support the use by optimal migration theory of (1) the flight-range equation modeled as a diminishing return function of added fuel mass and (2) the assumption of a U-shaped relationship between flight speed and flight power. Hedenström (2012) takes issue with my view that past and current data do not provide unequivocal support. He responds to my claim that "what is important is the diminishing return utility of the flight-range equation" and adds that "the increase in flight cost confirms the diminishing return utility of added fuel mass and, hence, that the fundamental flight-range equation is not compromised" (Hedenström 2012). He is certainly right: in the physical world in which we live, it is not possible to transport additional mass without spending additional energy (i.e., without performing extra work). My point was that when the fuel load of flying birds is low, the amount of additional energy spent is much lower than predicted by the fixed-wing aerodynamic theory. Because of this, the relationship between the potential flight range and fuel load, in spite of being a diminishing function—and I completely agree with Alerstam and Lindström (1990) and with Hedenström (2012) that it is a diminishing function—deviates much less from the direct proportionality than is assumed in the classical optimal migration theory.

As for the shape of the relationship between mechanical power required to fly and air speed (U-shaped, flat, or J-shaped), certainly the relationship is U-shaped if the range of air speeds experienced by flying birds during experiments is broad enough. The point is not whether the relationship is U-shaped under all air speeds physically achievable by a particular species—it certainly is. The point is whether the relationship is U-shaped under the range of air speeds that are routinely flown by the birds during their normal migratory flights.

Thus, in both cases, I do not challenge the basic physical relationships that Hedenström (2012) defends. I only question whether the deviations from direct proportionality in the case of the flight-range equation under small fuel loads (with which a large proportion of migratory flights happens), and from the flat form of the power–speed relationship under the air speeds usually flown, are indeed significant and influence the behavior of the migrants to a considerable extent. I am not the first to note these discrepancies between theory and practical considerations in the study of flying birds. For instance, Schmidt-Wellenburg et al. (2008) showed that Rosy Starlings (*Sturnus roseus*) could easily optimize their flight costs when extra load was added, and they cited other studies with similar results (Kvist and Lindström 2001, Engel et al. 2006, Schmidt-Wellenburg et al. 2007). Schmidt-Wellenburg et al. (2008:776) speculated that "birds could indeed always fly with a high efficiency and that efficiency does not change with mass, at least during the migratory season." They further suggested that aerodynamic considerations might not have met the reality of a flying bird, and that theory overestimated the effect of increased mass on flight costs. I simply proposed that these factors could be relevant for the optimal migration theory.

Hedenström (2012) suggests in his comments that my criticism of optimal migration theory (Chernetsov 2010) is not justified and that the optimal migration theory "will be further developed and refined." I completely agree with the latter opinion. We may differ in the choice of words (revision vs. development and refinement), but that is a secondary consideration to the primary conclusion, which is that I do not feel that our views on this subject differ to a substantial degree.