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Optimal Migration Theory: Response to Hedenström

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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.

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