

Optimal Migration Theory: Response to Hedenström

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- HEDENSTRÖM, A. 2008. Adaptations to migration in birds: Behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society of London, Series B* 363:287–299.
- HEDENSTRÖM, A. 2009. Optimal migration strategies in bats. *Journal of Mammalogy* 90:1298–1309.
- HEDENSTRÖM, A., AND T. ALERSTAM. 1995. Optimal flight speed of birds. *Philosophical Transactions of the Royal Society of London, Series B* 348:471–487.
- HEDENSTRÖM, A., AND T. ALERSTAM. 1996. Skylark optimal flight speeds for flying nowhere and somewhere. *Behavioral Ecology* 7:121–126.
- HEDENSTRÖM, A., AND T. ALERSTAM. 1997. Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. *Journal of Theoretical Biology* 189:227–234.
- KULLBERG, C., T. FRANSSON, AND S. JAKOBSSON. 1996. Impaired predator evasion in fat Blackcaps (*Sylvia atricapilla*). *Proceedings of the Royal Society of London, Series B* 263:1671–1675.
- KULLBERG, C., S. JAKOBSSON, AND T. FRANSSON. 2000. High migratory fuel load impair predator evasion in Sedge Warblers. *Auk* 117:1034–1038.
- KVIST, A., M. KLAASSEN, AND Å. LINDSTRÖM. 1998. Energy expenditure in relation to flight speed: What is the power of mass loss rate estimates? *Journal of Avian Biology* 29:485–498.
- PENNYCUICK, C. J. 2008. *Modelling the Flying Bird*. Academic Press, London.
- PENNYCUICK, C. J., A. HEDENSTRÖM, AND M. ROSÉN. 2000. Horizontal flight of a swallow (*Hirundo rustica*) observed in a wind tunnel, with a new method for directly measuring mechanical power. *Journal of Experimental Biology* 203:1755–1765.
- RAYNER, J. M. V. 1999. Estimating power curves of flying vertebrates. *Journal of Experimental Biology* 202:3449–3461.
- STEPHENS, D. W., AND J. R. KREBS. 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- TORRE-BUENO, J. R., AND J. LAROCHELLE. 1978. The metabolic cost of flight in unrestrained birds. *Journal of Experimental Biology* 75:223–229.
- WEBER, T. P., AND A. HEDENSTRÖM. 2000. Optimal stopover decisions under wind influence: The effects of correlated winds. *Journal of Theoretical Biology* 205:95–104.
- WEBER, T. P., T. ALERSTAM, AND A. HEDENSTRÖM. 1998. Stopover decisions under wind influence. *Journal of Avian Biology* 29:552–560.
- WIRESTAM, R., T. FAGERLUND, M. ROSÉN, AND A. HEDENSTRÖM. 2008. Magnetic resonance imaging for noninvasive analysis of fat storage in migratory. *Auk* 125:965–971.

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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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LITERATURE CITED

- ALERSTAM, T., AND Å. LINDSTRÖM. 1990. Optimal bird migration: The relative importance of time, energy, and safety. Pages 331–351 in *Bird Migration: Physiology and Ecophysiology* (E. Gwinner, Ed.). Springer-Verlag, Berlin.
- CHERNETSOV, N. 2010. Recent experimental data on the energy costs of avian flight call for a revision of optimal migration theory. *Auk* 127:232–234.
- ENGEL, S., H. BIEBACH, AND G. H. VISSER. 2006. Metabolic costs of avian flight in relation to flight velocity: A study in rose coloured starlings (*Sturnus roseus*, Linnaeus). *Journal of Comparative Physiology B* 176:415–427.
- HEDENSTRÖM, A. 2012. Recent experimental data on the energy costs of avian flight do not call for a revision of optimal migration theory. *Auk* 129:352–354.
- KVIST, A., AND Å. LINDSTRÖM. 2001. Basal metabolic rate in migratory waders: Intra-individual, intraspecific, interspecific and seasonal variation. *Functional Ecology* 15:465–473.
- SCHMIDT-WELLENBURG, C. A., H. BIEBACH, S. DAAN, AND G. H. VISSER. 2007. Energy expenditure and wing beat frequency in relation to body mass in free flying Barn Swallows (*Hirundo rustica*). *Journal of Comparative Physiology B* 177:327–337.
- SCHMIDT-WELLENBURG, C. A., S. ENGEL, AND G. H. VISSER. 2008. Energy expenditure during flight in relation to body mass: Effects of natural increases in mass and artificial load in rose coloured starlings. *Journal of Comparative Physiology B* 178: 767–777.

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